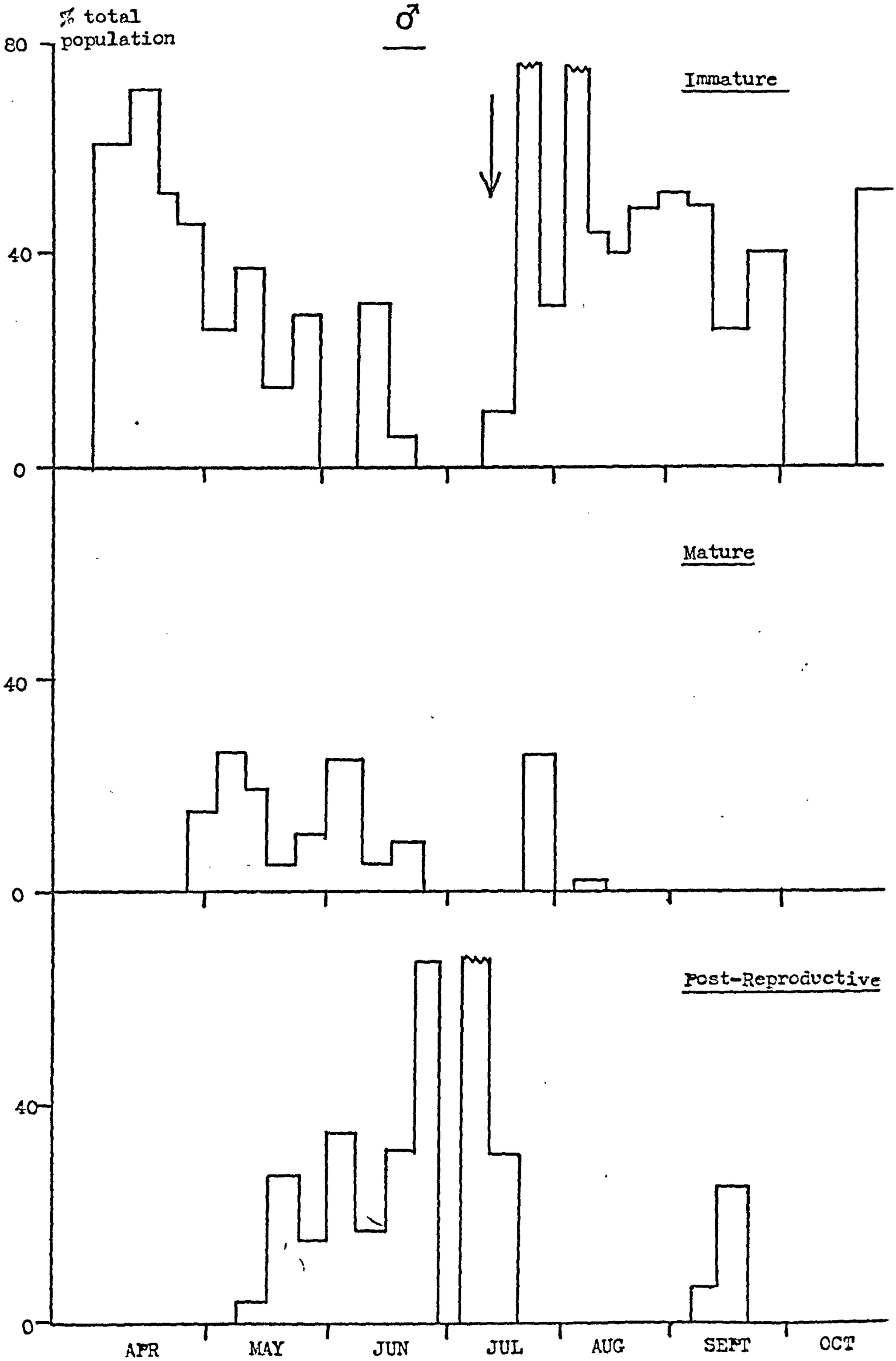

♂
% total population
80
40
0
Immature
Mature
40
0
Post-Reproductive
40
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

The Ecology of burying beetles

(*Necrophorus* : Coleoptera, Silphidae)

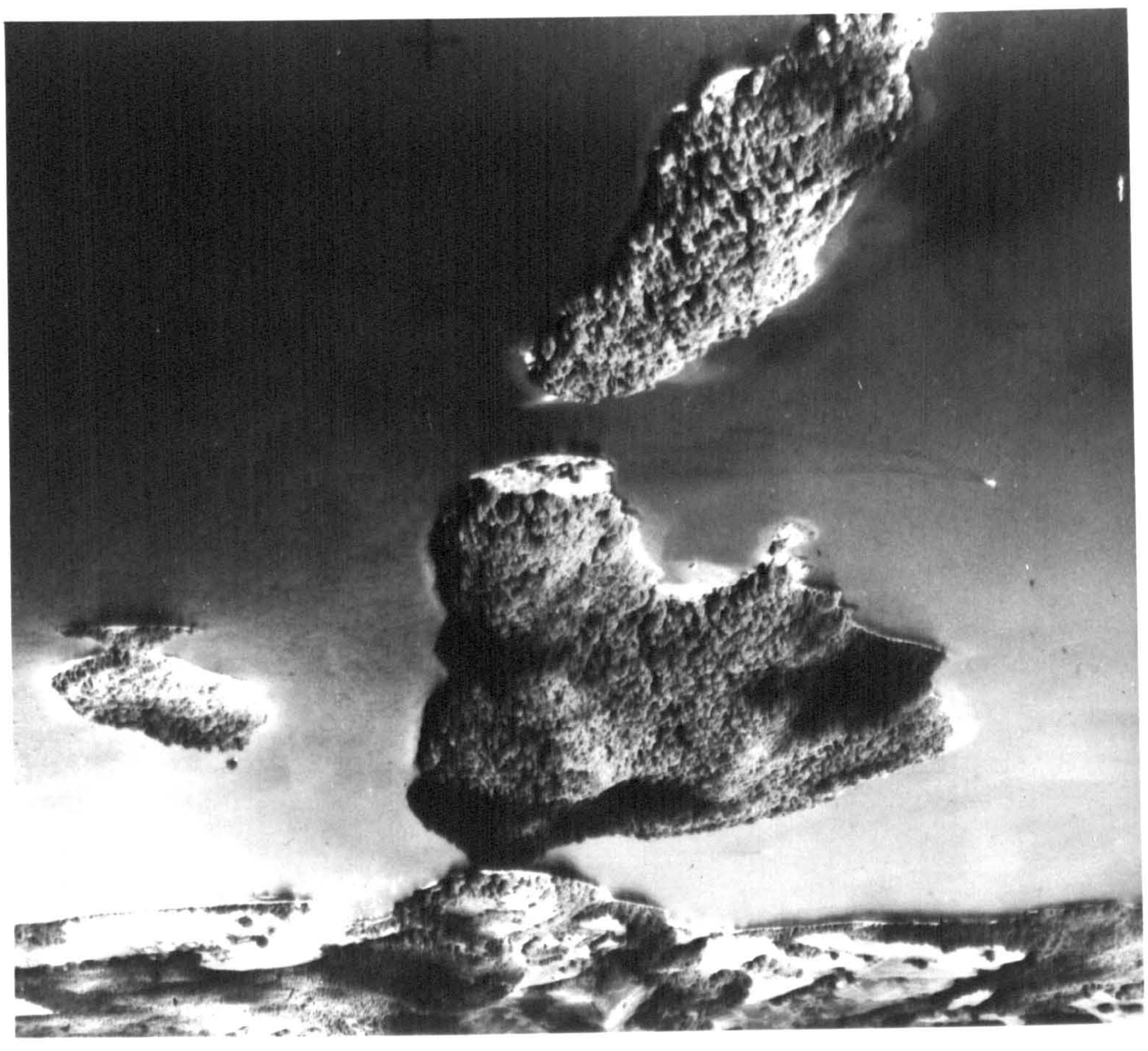
Cameron Easton B.Sc.

A Thesis submitted for the degree of Doctor of Philosophy at the University of Glasgow.

November 1979

Department of Zoology, University of Glasgow.

Inchcailloch from the South West.



ACKNOWLEDGEMENTS

It is a pleasure to thank Professor A.F.G. Dixon, who suggested the project, supervised throughout, and provided encouragement, constructive criticism and advice whenever it was required. The work was carried out in the University of Glasgow under a Natural Environment Research Studentship and I am grateful to Professor D.R. Newth for the facilities provided in the Department of Zoology and University Field Station.

Thanks are due to the Nature Conservancy Council for permission to work on Loch Lomond National Nature Reserve, and in particular to Mr. E.T. Idle who always managed to put the work into its true perspective. The Clyde River Purification Board kindly provided weather data for Arrochymore.

I am very grateful to Mrs. Susan Hughes for typing this thesis.

Special thanks are due to my wife Jill, who assisted with the diagrams and provided moral support throughout the writing-up period. Without her constant encouragement and patience, this thesis would never have been completed.

TABLE OF CONTENTS

SUMMARY

1. An ecological study of the burying beetles (*Necrophorus*, Coleoptera: Silphidae) was carried out in the oak woodlands of Loch Lomond.

2. Three species of burying beetles were found in the study area : *Necrophorus vespilloides*, *N.humator*, *N.investigator*.

3. A population study on the island of Inchcailloch showed that *N.vespilloides*, the most abundant species, bred from April until July as did *N.humator*. The offspring of these breeding adults appeared in the population from July to September. This life cycle led to two peaks in population number. *N.investigator* bred from July to September. As the offspring of the breeding population overwinter as prepupae, only one peak in population numbers was observed.

4. The size of the second peak in population numbers of *N.vespilloides* varied from year to year. It is proposed that this was due to variations in breeding success between years. Breeding success also varied between Inchcailloch and the mainland.

5. *N.investigator* emerged earlier on the mainland than on Inchcailloch.

6. The number of eggs in mature *N.vespilloides* was 13, and in *N.investigator* 9.83. Post reproductive females retained a number of eggs in the ovarioles.

7. The size of the fat reserves of immature *N.vespilloides* at the end of the season varied from year to year. When beetle numbers were high fat reserves were low, and when low, fat reserves were high.

8. Mark/recapture studies showed that both emigration from and immigration to Inchcailloch were low, less than 11% of the population. The rate of movement of beetles to and from the mainland was much higher.

9. Experimental studies on interspecific competition were carried out at Rossdhu, on the west side of the loch.

10. N.humator does not compete with the other species, as it uses larger corpses for breeding.

11. Adult N.vespilloides and N.investigator are present at the same time, for about a month, and during this time bury the same type of corpse.

12. The proportion of corpses buried by N.vespilloides and N.investigator on their own is reduced in the presence of the other species. N.vespilloides buries fewer corpses than does N.investigator when the two species are together, and in the laboratory, N.investigator buries all corpses. It is suggested that N.investigator is a stronger competitor than N.vespilloides.

13. Results from the population study suggest that the appearance of N.investigator is associated with the end of breeding by N.vespilloides.

14. There is some evidence that a preference for rat sized corpses may be shown by N.investigator when a choice is offered. Interspecific competition is unlikely to be avoided in this way as both mice and rats are buried by N.investigator, a direct choice of corpses will not occur in the field, and rat sized corpses are not present in the study area.

15. The evidence for interspecific competition is discussed. It is concluded that there is potential for interspecific competition, and some evidence that competition may actually occur, although this evidence may be interpreted otherwise.

16. The relationship between burying beetles and corpses was studied experimentally at Rossdhu, and in the laboratory.

17. N.vespilloides lays all the eggs it matures on mice and rats. N.investigator lays all its eggs on rats, but lays fewer eggs on mouse corpses than are matured.

18. In the field, mortality during development was normally 27% for N.vespilloides and 35% for N.investigator. Stages in the soil had the highest mortality, while mortality within the corpse was very low, less than 2%.

19. In normal clutches there was no relationship between developmental mortality and clutch size.

20. In artificially increased clutches there was a density dependent relationship between clutch size and mortality, above a threshold egg density. Actual clutch size was always below the theoretical threshold density.

21. Reduction in corpse size led to a reduction in threshold density and in mean clutch size. It is proposed that the beetles assess the carrying capacity of the corpse and alter the number of eggs laid accordingly. Excess eggs are retained in the ovarioles.

22. Fluctuations in air temperature were reduced by the crypt so that conditions in the corpse remained stable. It is proposed that this helps to reduce mortality of the stages within the corpse.

23. Without food, newly emerged beetles die within 5 - 7 days.

24. Burying beetles were ready to take food other than carrion. Regular feeding on such material prolonged survival time indefinitely and led to weight increases. It is proposed that burying beetles in the field normally feed on soft bodied invertebrates.

25. There are more burying beetles in the population than there are corpses available, and so part of the population does not breed. Due to the low mortality, individuals which do breed produce sufficient offspring to maintain the breeding population and provide

an excess for the following year. An excess population is necessary to ensure that maximum use is made of a highly variable and unpredictable resource.

26. The adaptations of Necrophorus that enable it to deal with carrion are discussed. Despite living in a typical temporary habitat, many of the adaptations of burying beetles are those of a K-strategist, due to modification of the resource by the beetle.

SECTION 1.

GENERAL INTRODUCTION

1. GENERAL INTRODUCTION

Burying, or Sexton, beetles are common names for members of the genus Necrophorus (Fab.) - Coleoptera : Silphidae. There are 61 species in the genus, with a worldwide distribution outwith tropical and polar regions (Portevin, 1926a). There is disagreement over how many species are present in Britain. The species cited by different authors are listed in Appendix 1. Kloet and Hinks (1945) give seven species of burying beetle in Britain (Table 1:1), and their terminology will be followed in this study.

Four species of Necrophorus have been recorded from the Clyde area : N.humator, N.vespilloides (also called N.mortuorum), N.investigator (also called N.ruspator) and N.vespillo (Elliot, Laurie and Murdoch, 1901; Welch, 1968; R.A. Crowson, pers. comm.). Only the first three were found during this study (fig. 1:1).

Unlike other insects which feed and breed on carrion, Necrophorus buries a corpse as a source of food for its larvae. It is this behaviour which has given burying beetles their common name. Fabre (1919) was the first to describe the complex behaviour of these insects. Pukowski (1933) confirmed many of these observations and supported them with quantitative data. The descriptions given by these authors remain the definitive studies of the habits of burying beetles and are often quoted.

As a preliminary to the more detailed studies described in this work, the reproductive behaviour and life cycle of Necrophorus, as described by Fabre (1919) and Pukowski (1933), are briefly summarised. The literature on burying beetles is then reviewed.

Table 1:1

British Necrophorus species. (From Kloet and Hinks 1st Edition 1945).

Necrophorus	germanicus	Linnaeus	1758
N.	humator	Goeze	1777
N.	vespilloides	Herbst	1783
N.	vestigator	Herschel	1807
N.	investigator	Zetterstedt	1824
N.	interruptus	Stephens	1830
N.	vespillo	Linnaeus	1758

Fig. 1:1

Necrophorus species found in the study area.

N. vespilloides

N.humator

N.investigator

Behaviour, reproduction and life cycle

Burying beetles are powerful fliers and are attracted to a corpse by the odour of decomposition. If males reach a corpse first they adopt a 'sterzeln' position, when they are believed to emit a pheromone. This is alleged to attract females to the corpse, where mating occurs. Intraspecific competition may occur between individuals or pairs for possession of the carcass, and this may involve stridulation. Eventually, a female, or male-female pair, possess the corpse. The losers are driven off or killed and eaten. The successful female, or pair, then buries the corpse (fig. 1:2a, b). This is done by the beetle, or beetles, removing the soil from underneath the corpse. They dig with their fore legs and push loose soil away with their hind limbs (fig, 1:2a, b). The corpse sinks into the hole so excavated (fig. 1:2c, d), and as it sinks is rolled and compressed into a ball (fig. 1:2d, e).

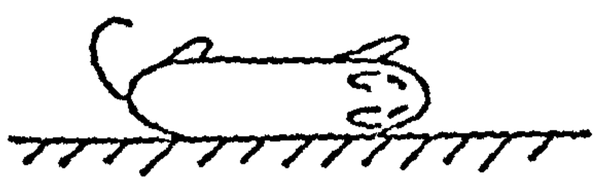
The corpse is buried from 6-10cm deep in a chamber or crypt. The walls of the crypt are completely smooth. During burial, fur or feathers are stripped from the corpse and incorporated into the walls of the burial chamber. The reason for this is uncertain, although it may strengthen the walls of the crypt. Removal of fur may remove any adhering blowfly eggs, or may allow larvae easier access to the corpse. The female digs a side tunnel off the main crypt in which she lays her eggs (fig. 1:2g). After egg laying, the male normally leaves but females always stay with the corpse.

On hatching, the larvae crawl to the crypt, guided by the stridulations of the female (Neimitz and Krampe, 1972). There are three larval instars (fig. 1:2i) and the female feeds the early stages of each instar on regurgitated crop contents (fig. 1:2h), presumably while the mouthparts of the larvae are still soft after each moult. Although she

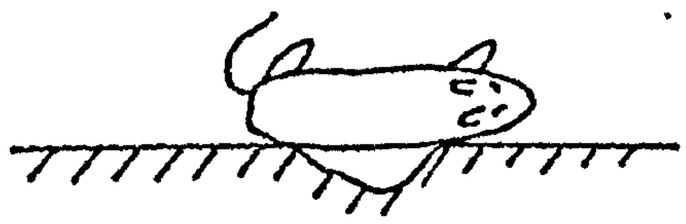
Fig. 1:2

Burial of a corpse by Necrophorus

a.



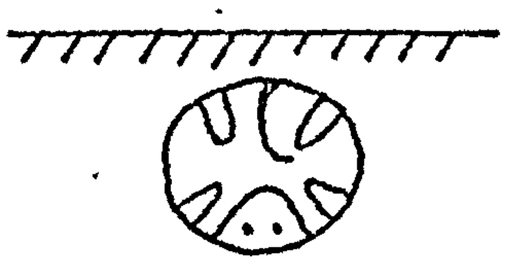
b.



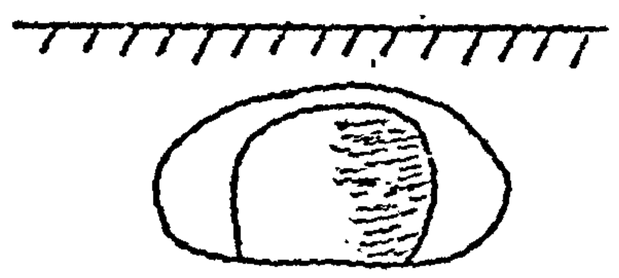
c.

d.

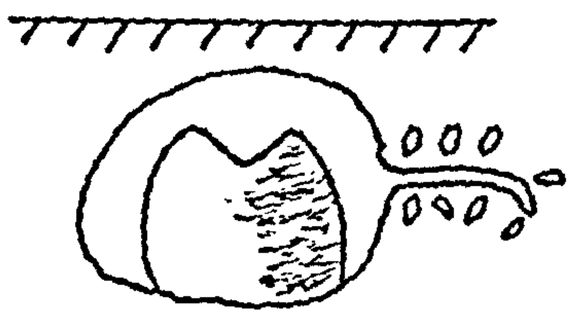
e.



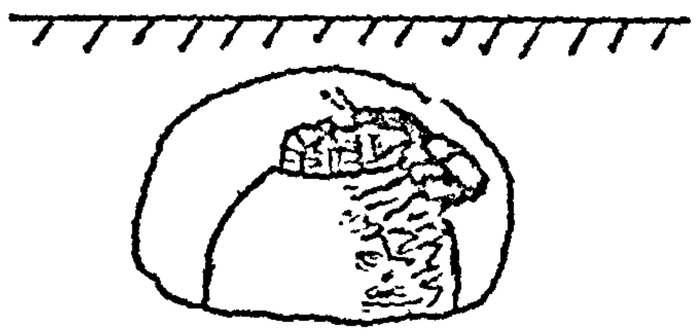
f.



g.

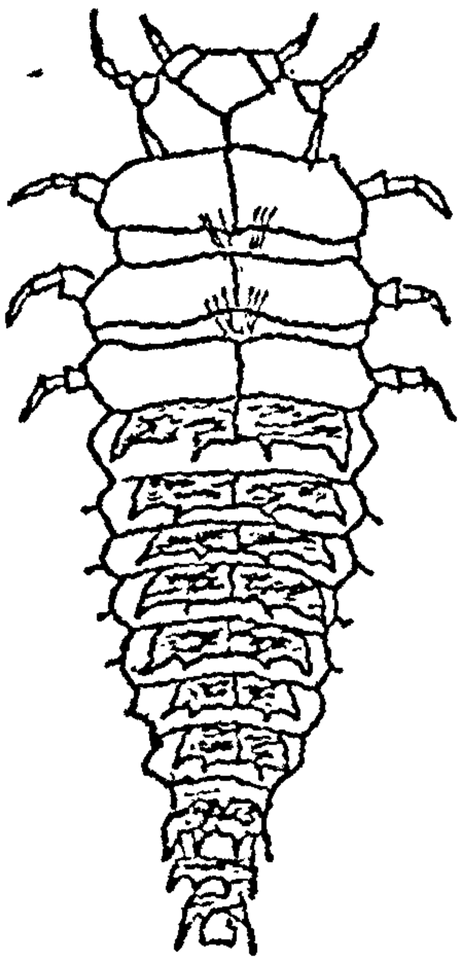


h.

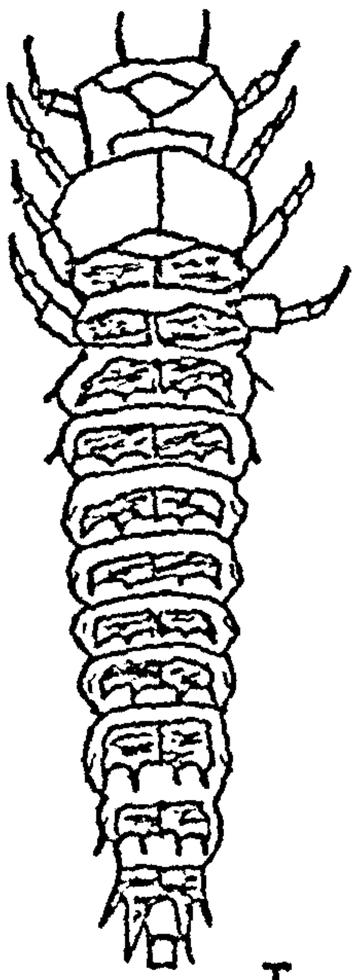


i.

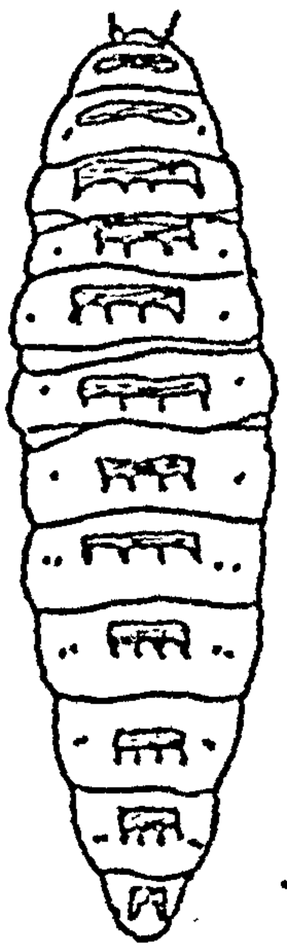
I



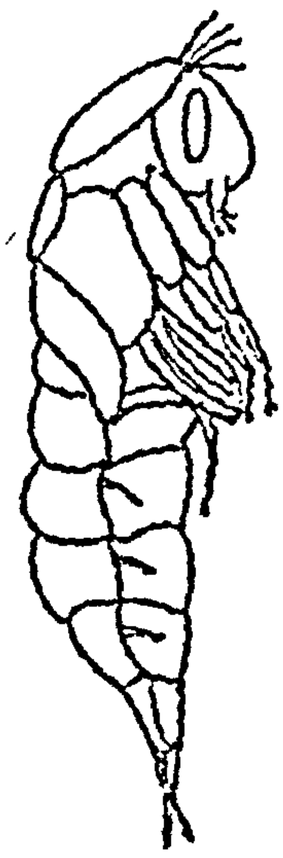
II



III



pupa



feeds the larvae, the female herself is not believed to feed while in the crypt (Springett, 1967). At the end of the third instar the larvae stop feeding, disperse from the corpse, form a chamber in the soil and pupate (fig. 1:2i). The pupae give rise to adults which emerge from the soil while the cuticle is still soft (callow adults). As far as is known, all species of Necrophorus behave in this way.

Burying beetles have two types of life cycle. In the first, immature adults spend the winter in diapause, emerge in spring when they feed and mature their gonads (fig. 1:3a). Breeding occurs in April, May and early June. Immature adults of the next generation appear in August and September, feed to build up their fat reserves and go into diapause for the winter. In the second type of life cycle (fig. 1:3b) adults emerge fully mature in summer, breed in July and August, overwinter in the soil as prepupae, pupate in late spring and emerge as mature adults in July. In both types of life cycle, breeding is believed to occur only once each year.

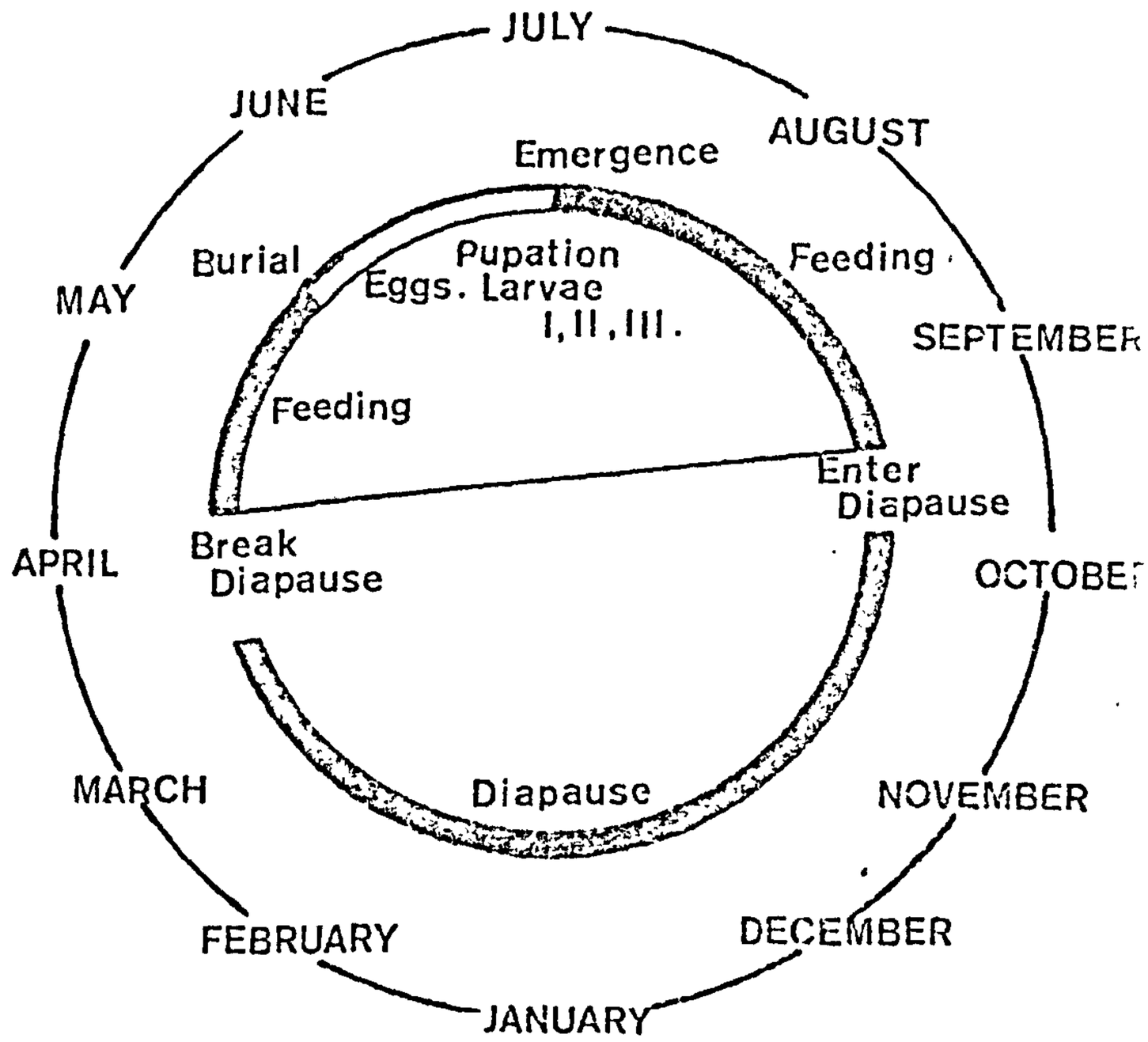
Review of literature

The presence of Necrophorus on carrion has been frequently noted during studies of succession (Kaufmann, 1931; Walsh, 1931. 1933; Moore, 1955; Millican, 1965; Hussey and Lane, 1967; Likovský, 1967; Payne, 1967; Shubeck, 1967; Ratcliffe and Leudtke, 1969; Vaughtholme-Jensen, 1971). They arrive early in the succession, leaving when other insects, particularly blowfly larvae, become common. In addition to these records of the presence of Necrophorus, lists have been compiled of the species present in particular localities : Ireland (Johnson and Halbert, 1902); Germany (Reitter, 1909; Delahon, 1925); Pamirs (Kieseritzsky, 1930); Barbary (Peyerimhoff, 1934); Nebraska, U.S.A. (Meserve, 1936); Spain (Pessôa and Lane, 1941); Loch Lomond, Scotland

Fig. 1:3

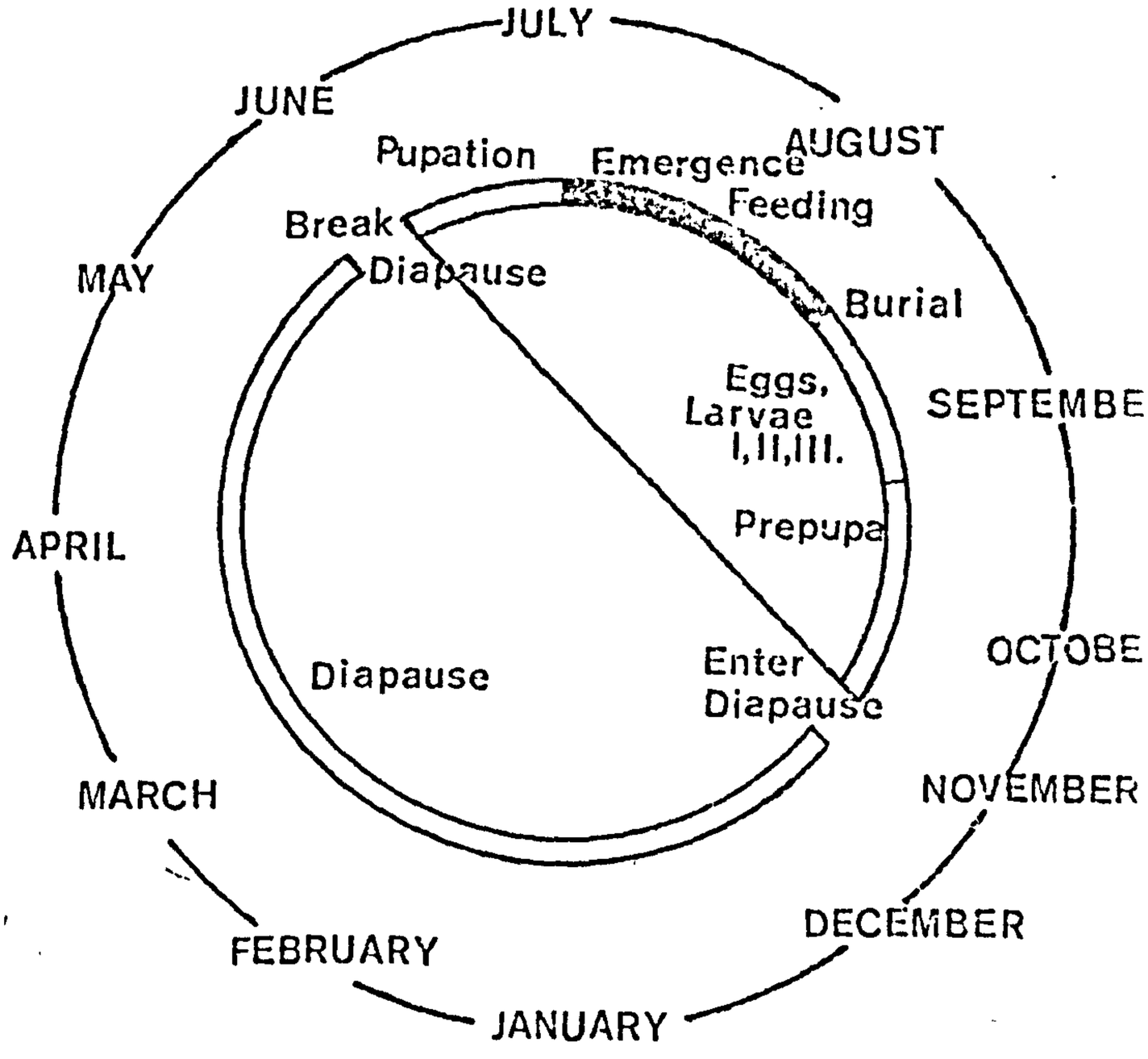
Life cycles of Necrophorus

A).



N. germanicus
N. humator
N. vespilloides
N. vestigator
N. vespillo

B).



N. investigator
N. interruptus

Adult stages

Larval stages

(Welch, 1968); Yugoslavia (Mikšić, 1971); France (Toulon, 1971); Monks Wood, England (Welch, 1973); Iberian Peninsula (Pardo-Alcaide and Yus, 1974).

Descriptions and nomenclature of new species are common (Portevin, 1926b; Hatch, 1925, 1927a; Hlisnikowski, 1932, 1964a; Arnett, 1946a, 1950; Mazokhin-Porshnyakov, 1953; Mroczkowski, 1959; Shibata, 1969, Kryzanovskiy, 1971), and aberrations are also described (Jacobson, 1924; Kôno, 1929; Hlisnikowski, 1929, 1942; Pic, 1933; Roubal, 1934, 1939, 1942; Kanaki, 1935; Leech, 1937; Portevin, 1943; Smetana, 1948; Székessy, 1961; Kamimura, Nakana and Koyama, 1964; Emetz and Schawaller, 1975). A more general systematic treatment of the species of Necrophorus and summary of the literature is to be found in Portevin (1926a). Hatch (1932) and Herman (1964) consider that 'Nicrophorus' is the correct spelling. The systematics of the genus Necrophorus are discussed by Hatch (1927b, 1928), Lemenov-Tian-Shanskii (1933), Arnett (1946b, 1947) and Théorides (1950a) but the major systematic works are by Horn (1880) and Arnett (1944). The latter work was critised by Hatch (1946). Several Russian authors create new genera and sub genera on the basis of morphological characters alone, for example Schlegoleva-Barovskaya (1933) Hlisnikowski (1964b). Hatch (1940) describes the systematics of Necrophorus vespilloides and Brivio (1953) N.germanicus.

The morphology of adult Necrophorus has been described by Šulc (1940) - mouthparts and legs, Hlavac (1975) - prothorax, and Bliss (1949) - secondary sexual characteristics. In the Necrophorini, three types of ovipositors are distinguished by Gersdorf (1970) namely : Acanthopsilus type, N.investigator type and N.vespillo type. These correspond to phylogenetic relationships within the Necrophorini, and to the two types of life cycle shown by individuals of the genus

Necrophorus. Larval morphology has been described by Pukowski (1934a) and Lengerken (1938), larval development of N.vespillo and N.fossor by Roussel (1964a, b) and colour patterns by Hinton (1969).

Gersdorf (1969) has described the fossil species N.pliozaenicus from the Upper Tertiary of North Germany. Sidor (1970) observed that rabies virus in infected corpse material was inactivated after ingestion by burying beetles. Kay, Rothschild and Aplin (1969) describe rectangular particles, 10-15 mu in size, in the haemolymph of the thorax of N.investigator, but do not say what they might be. A technique for capturing Necrophorus, among other species, is given by Newton and Peck (1975). Schneider (1975) described the flight of burying beetles. Prokopic and Svatopluc (1975) found that N.humator, N.interruptus, N.vespillo and N.vespilloides act as intermediate hosts for several species of helminth.

Descriptions of the behaviour of these large insects are relatively infrequent. Observations on the activity of burying beetles (Shubeck, 1970, 1971) or burying behaviour (Steele, 1927; Abbot, 1937; Milne and Milne, 1944, 1976; Ling, 1957; Tweedie, 1964) have added little to the detailed knowledge provided by Fabre (1919) and Pukowski (1933). Wilson (1971, 1975) uses Pukowski's observations to discuss Necrophorus in relation to pther social insects, and classifies burying beetles as 'pre-social'. Social behaviour and parental care in Necrophorus has been discussed by Pukowski (1934b, c), Mosebach-Pukowski (1936) and Lengerken (1939).

Sound production by Necrophorus has been known for some time (Dumortier, 1963), and has been studied by Niemitz (1972) and Niemitz and Krampe (1971, 1972). Pukowski (1933) suggests that sound production

has a role in communication in Necrophorus. Sounds are complex, and can be modified by the individuals producing them, in response to the sounds made by other individuals. Sounds are emitted during fighting between adults, and when larvae hatch. Freshly hatched larvae are sensitive to the sounds made by females (Niemitz and Krampe, 1972). The structures used for sound production are the abdominal file and elytral plectrum (Niemitz, 1972). N.vespilloides, N.humator and N.investigator show differences in the structure of the stridulatory apparatus, which have been attributed to the species specific nature of sound communication (Schumacher, 1973). When disturbed, burying beetles emit a buzzing, which is regarded as Mullerian mimicry of bumble bee sound (Lane and Rothschild, 1965).

Necrophorus locate carrion by smell. Tests have been made on the responsiveness of burying beetles to odours of various types (Abbott, 1927a, b; Shubeck, 1968), and the sense organs on the antennae involved in olfaction have been studied (Dethier, 1947; Wasowska, 1953). Ernst (1964, 1972a, b) has examined the olfactory sensilla under the electron microscope and distinguished two types on the basis of their morphology - basiconic and coelosphaeric. The development of the basiconic sensillum was studied microscopically. Electrophysiological studies on the basiconic sensillum reveal sensitivity to various mechanical and chemical stimuli (Boeckh, 1962a, b). Coelosphaeric sensilla are responsible for coding the odour of carrion (Waldow, 1973). When these sensilla are destroyed, basiconic sensilla still respond to the odour of carrion but the beetle is unable to orientate - i.e. the beetle smells the carrion, but cannot act on the information. As long as the coelosphaeric sensilla are functional, beetles will respond to carrion, even when the basiconic sensilla, which make up 90% of the sense cells, are destroyed.

Relatively few studies have been made on the ecology of Necrophorus. The life cycles of various species have been studied by Pukowski (1933, 1934c), Leech (1935) and Sidor (1967). Numbers caught in the field have been recorded by Kaufmann (1941), Paulian (1946), Mroczkowski (1949) and Shubeck (1969). Petrŭska (1964) studied flight activity and the distances travelled by burying beetles, using marked individuals, which revealed that they can travel up to 4km in 24 hours. The symbiotic relationship between Necrophorus and the mite Poecilochirus necrophori (Vitzh) was studied by Starzyk (1967) and Springett (1968), who showed that both species are dependent on the presence of the other for successful breeding. Commensal nematodes, mainly Rhabditids, have been recorded by Volk (1950) and Théorides (1955). Nickle (1970, 1972, 1973) also describes true parasitic nematodes of burying beetles which cause reduced egg production, or complete sterility in infected individuals. Roussel (1963, 1965) concluded that temperature and photoperiod have little effect on the termination of diapause which is controlled by internal factors in Necrophorus fossor and N.vespillo. Adult Necrophorus humator and N.vespillo prefer temperatures of 11-23°C and high humidity (Théorides and Van Heerdt, 1952), which correlate with the habitats these beetles occupy in the field. Paulian (1946), Cantonnet and Lecordier (1947), Roehrich (1949) and Théorides (1950b) suggest that interspecific competition is avoided by the different species living in different habitats. Changes in seasonal abundance are associated with the life cycles of the various species (Théorides, 1950b).

There have been only two attempts to study the ecology of Necrophorus populations. Novák (1964a, b, 1965a, b) claims that seasonal abundance and variations in numbers have been associated with differences in life cycles and weather and interspecific competition is

avoided by habitat segregation and life cycle differences. Springett (1967) studied interspecific relations between Necrophorus investigator and N.humator on Inner Farne island. Estimates were made of the size of the population of each species, and variation in population size were related to the main carrion source - tern chicks. This is one of the few studies to be carried out on British burying beetles, and the only quantitative analysis of their ecology.

Aims of this study

Some gaps are apparent in our knowledge of the ecology of burying beetles. It is not known how relevant are the observations made by Springett (1967) on the treeless Inner Farne to the complex ecosystem of an oakwood. Therefore, basic studies are required to test if the results obtained from other areas are applicable to the burying beetle populations of oakwoods. Little attention has been paid to relations between individual burying beetles and the resources utilised by them for feeding and breeding. Information on this is necessary before the effect of resources on populations can be assessed. Few attempts have been made to study the relationships of different Necrophorus species living in the same habitat and how they may coexist. Such a study is basic to an understanding of the distribution and abundance of burying beetles. Fihally, no one has as yet attempted to explain how a population of burying beetles might be regulated. Although a long term study is necessary to determine what regulates a population, factors which influence numbers may be discovered during the course of a short term study.

The aim of this research is to fill these gaps in our knowledge of the ecology of Necrophorus. To this end, the main objectives of the study were :

a) To describe the composition and seasonal abundance of burying beetles in an oakwood.

b) To investigate the interactions between the Necrophorus species living in the study area.

c) To determine the relationship between the various species of Necrophorus and the carrion available to them.

d) To identify factors which might influence population numbers, and assess their effect.

Little information is available on burying beetle populations, and so much of the study was devoted to compiling basic data on the ecology of the populations present in the oakwoods.

SECTION 2.

ANALYSIS OF A POPULATION IN THE FIELD

2. ANALYSIS OF A POPULATION IN THE FIEID

2.1. Introduction

The area chosen for the population study was the island of Inchcailloch, part of Loch Lomond National Nature Reserve. This area is representative of much of the oakwood round the shores of Loch Lomond. Although accessible, the island is relatively free from human disturbance, and so is suitable for prolonged sampling. There are no large mammalian scavengers, which frequently remove bait set out in other areas. The boundaries of the trapping area are easily defined. Much information is available on the island, due to its National Nature Reserve status. Finally, the area is convenient for access from the University of Glasgow Field Station and was close to other experimental areas. No experiments were carried out in the population study area.

The aim of the population study was to trap burying beetles, record the structure of the population and return marked individuals to the population for mark/recapture analysis. The population study was carried out from March 1973 until August 1975.

2.2. Materials and Methods

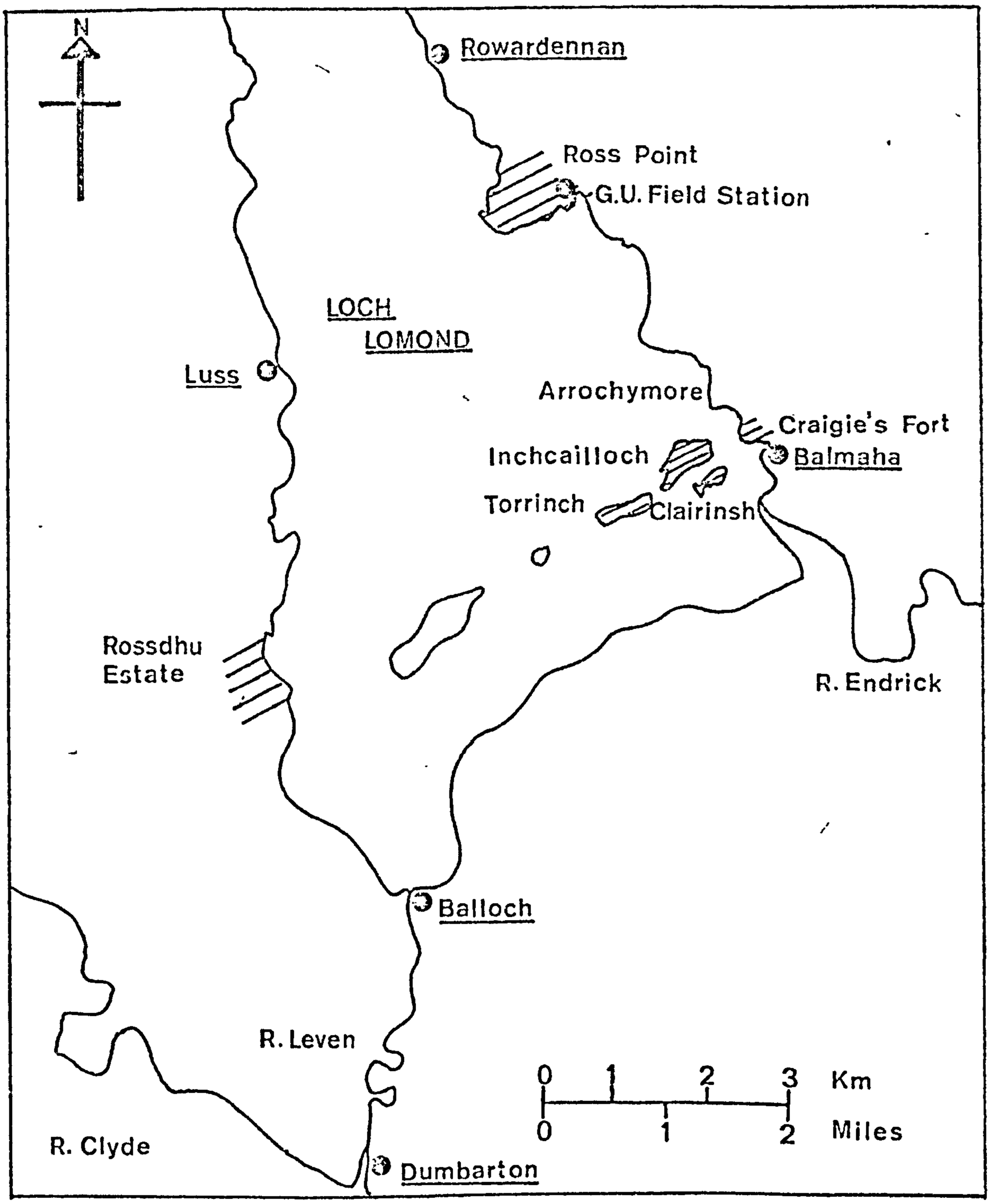
2.2.1. Description of Sampling area.

The main population study was carried out on the island of Inchcailloch (NS 410905). Traps were also set on the adjacent islands of Torrinch (NS 402895) and Clairinsh (NS 413900), and on a nearby area on the mainland at Craigie's Fort (NS 416903) (fig. 2:1).

Inchcailloch lies about 200m from the mainlahd and has an area of 54ha. The island lies on the Highland Boundary Fault line and consists of two parallel ridges joined by a watershed (fig. 2:2). The higher, southern ridge is formed by conglomerate and the lower, northern

Fig. 2:1

Study areas on Loch Lomondside

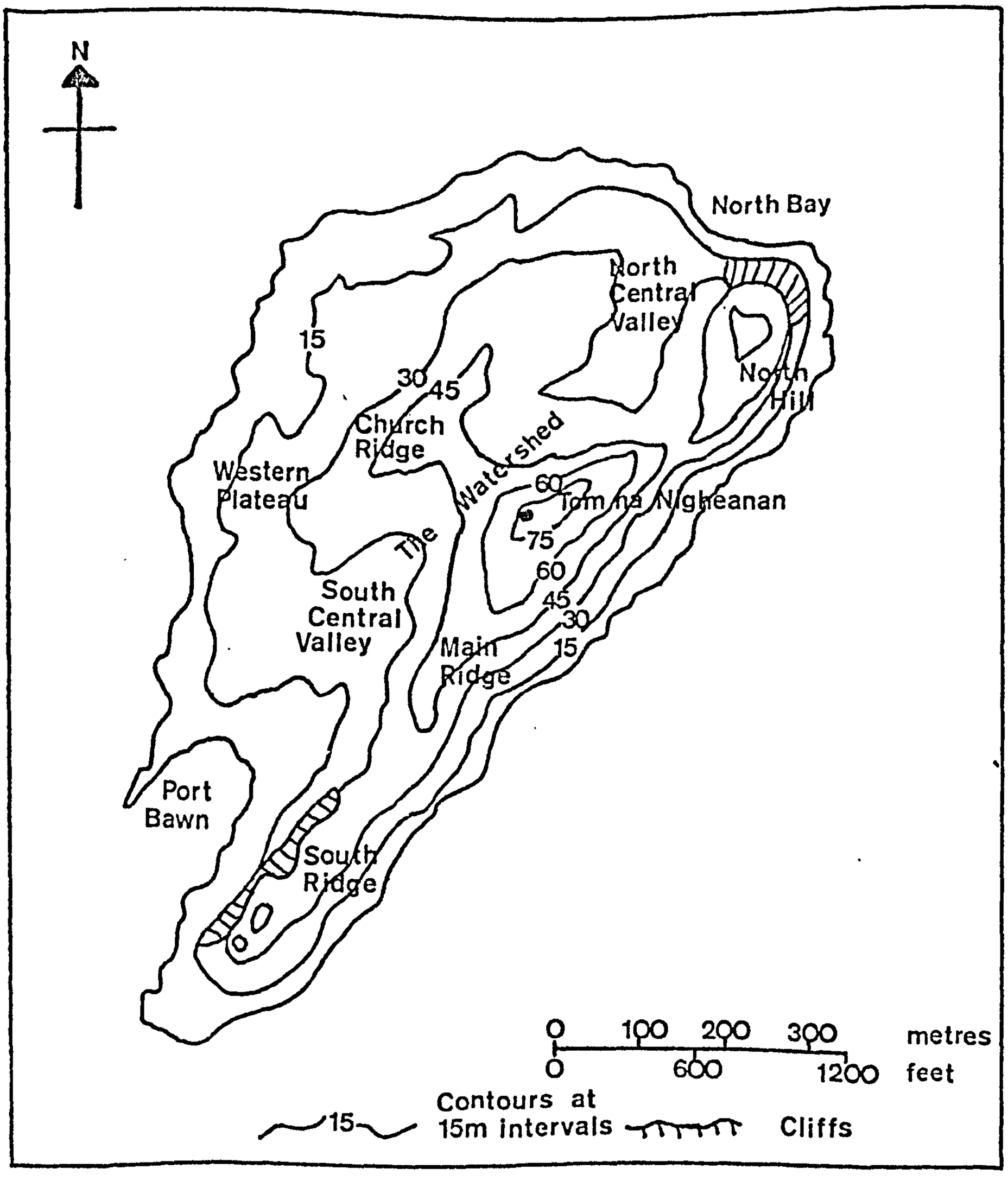

N
Rowardennan
Ross Point
G.U. Field Station
LOCH
LOMOND
Luss
Arrochymore
Craigie's Fort
Inchcailloch
Balmaha
Torrinch
Clairinsh
Rossdhu
Estate
R. Endrick
Balloch
R. Leven
0 1 2 3 Km
0 1 2 Miles
R. Clyde
Dumbarton

/// Study areas

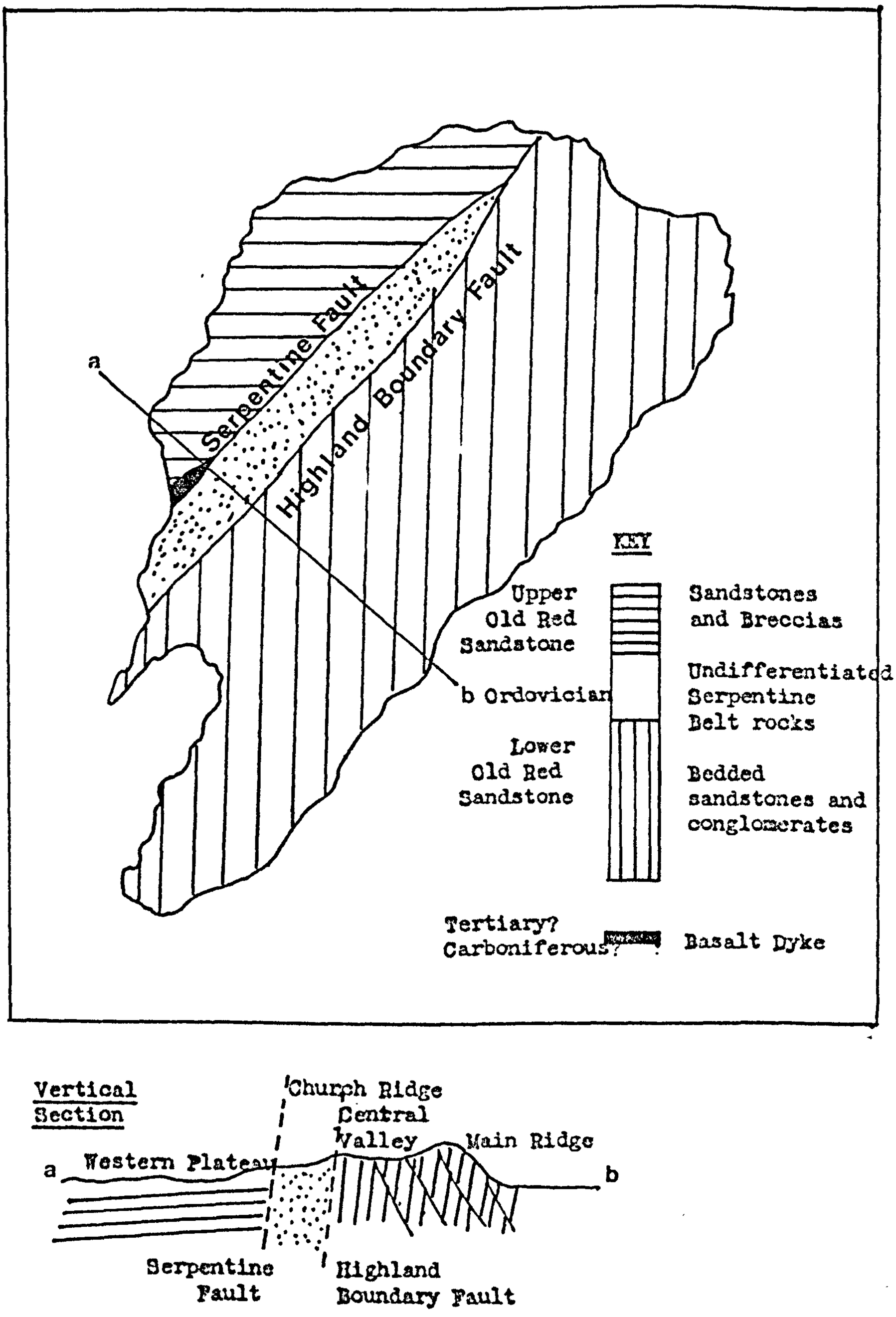
Fig. 2:2

Inchcailloch : Physical features.

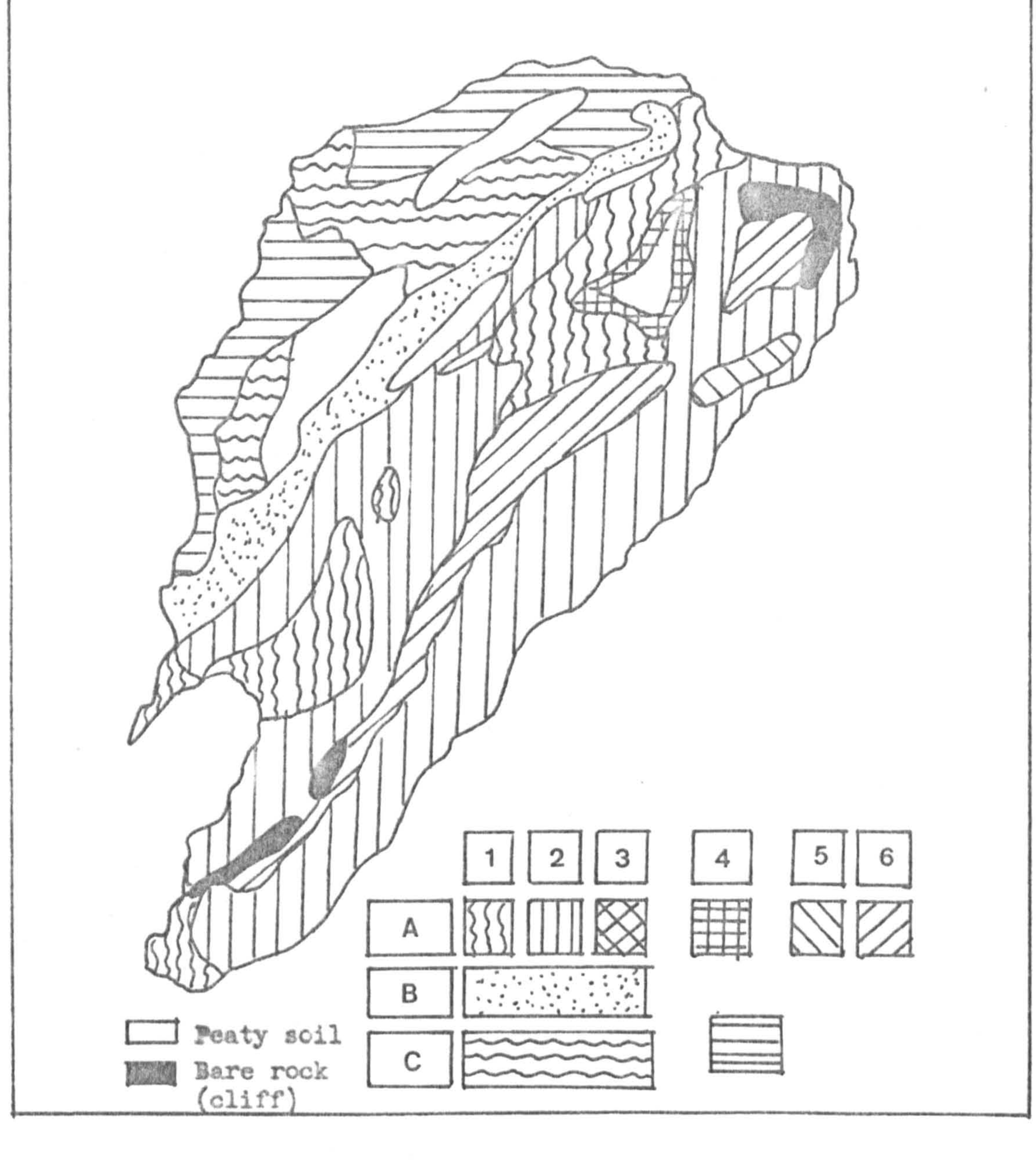
a. Topography



b. Geology


a
Serpentine Fault
Highland Boundary Fault
b Ordovician
KEY
Upper Old Red Sandstone
Sandstones and Breccias
Undifferentiated Serpentine Belt rocks
Lower Old Red Sandstone
Bedded sandstones and conglomerates
Tertiary? Carboniferous?
Basalt Dyke
Vertical Section
Church Ridge
Central Valley
Main Ridge
a
Western Plateau
b
Serpentine Fault
Highland Boundary Fault

c. Soils



A	Lower Old Red Sandstone and Conglomerates	1	Brown Earth
B	Serpentine rocks	2	Brown Podzol
		3	Brown Ranker
C	Glacial drift	4	Gleyed Brown Earth
		5	Iron Podzol
		6	Iron Ranker

ridge by serpentine (Rosen, 1963). Differences in geology and drainage lead to local variation in the soils of the island, which are, however, all in an acid, base-poor category (Hornung and Mew, 1970). Over much of the island, climatic conditions and low grazing pressure have led to the development of oakwood (Horrill, Sykes and Idle, 1975). Oak (Quercus robur L. and Quercus petrea Seibl) and birch (Betula pubescens Ehrh.) form the canopy, with an understory of rowan (Sorbus aucuparia L.), hazel (Coryllus avellana L.) and holly (Ilex aquifolium L.). Alder (Alnus glutinosa Gaertn) and ash (Fraxinus excelsior L.) occur in less well drained areas. The ground flora consists largely of bracken (Pteridium aquilinum Kuhn), woodrush (Luzula sylvatica Gaud.), bramble (Rubus fruticosus agg.), honeysuckle (Lonicera periclymenum L.), bluebell (Endymion non-scriptus Garcke), wood sorrel (Oxalis acetosella L.), buckler fern (Dryopteris dilatata ..Gray) and hard fern (Blechnum spicant Roth). In wetter, or more base rich areas, enchanter's nightshade (Ciraea lutetiana L.), dogs mercury (Mercurialis perennis L.), golden saxifrage (Chrysosplenium oppositifolium L.) and creeping buttercup (Ranunculus repens L.) are found. Pine (Pinus sylvestris L.) and larch (Larix decidua Mill) are the dominant trees on the thin acid soils at the summits of the south ridge and here the ground flora consists of ling (Calluna vulgaris Hull), heather (Erica cinerea L.) and blaeberry (Vaccinium myrtillus L.). In general terms the vegetation of Clairinsh and Torrinch is similar to that of Inchcailloch. Craigie's Fort resembles the summits of the south ridge of Inchcailloch, with pine, blaeberry and bracken. This area is considerably affected by human visitors.

Inchcailloch is ornithologically rich, with breeding bird densities of 1600 pairs per km^2 on the west side of the island and 1230 pairs per km^2 on the east (Williamson, 1974). Bank voles (Clethrionomys

glareolus Schr.) appear to be the most numerous small mammal, with short-tailed voles (Microtus agrestis L.) and common shrews (Sorex araneus L.) also present (East, 1964; Placido, 1971). Roe deer (Capreolus capreolus L.) and fallow deer (Dama dama L.) occur on the island (Idle and Mitchell, 1968; Theaker, 1976, 1977). A number of grey squirrels (Sciurus carolinensis Gm.) are also present.

The invertebrates of Inchcailloch have not been studied systematically. There are some species lists (eg. Curtis, 1976) but none are of relevance to this study.

A weather station is operated at Arrochymore (NS 410913) about 1 km north of Inchcailloch (fig. 2:1). Data from this station have been kindly made available by the Clyde River Purification Board. The temperature and rainfall recorded over the period of the study is shown in fig. 2:3 and summarised in Table 2:1 (April to July of each year) and Table 2:2 (July - September). It is assumed that the weather conditions on Inchcailloch will be similar to those recorded at Arrochymore.

2.2.2. Sampling techniques.

Trapping grid:

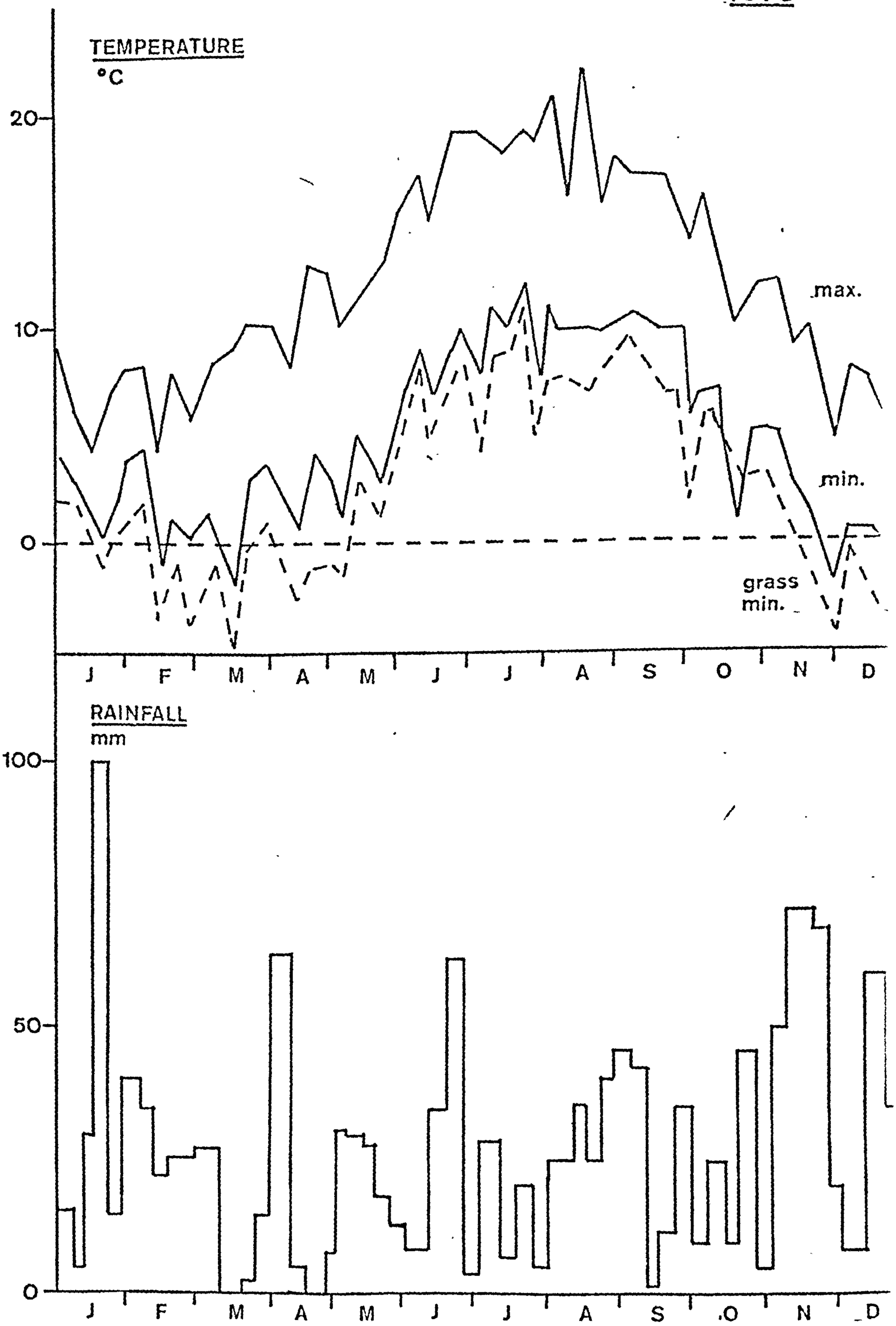
Fifty one baited traps were put out 100m apart on Inchcailloch 4 on Clairinsh, 3 on Torrinch and 3 on the mainland (fig. 2:4). The trap consisted of a 1 lb Kilner jar with a plastic cover (fig. 2:5). The jar contained pieces of rat, weighing about 40 gms, or whole 3-day old chicks which weighed about 60 gms. The bait was changed every 2-3 weeks. Beetles could enter the trap, through the hole at the top, but were unable to leave. To prevent starvation, beetles could feed on the carrion while in the trap.

Fig. 2:3

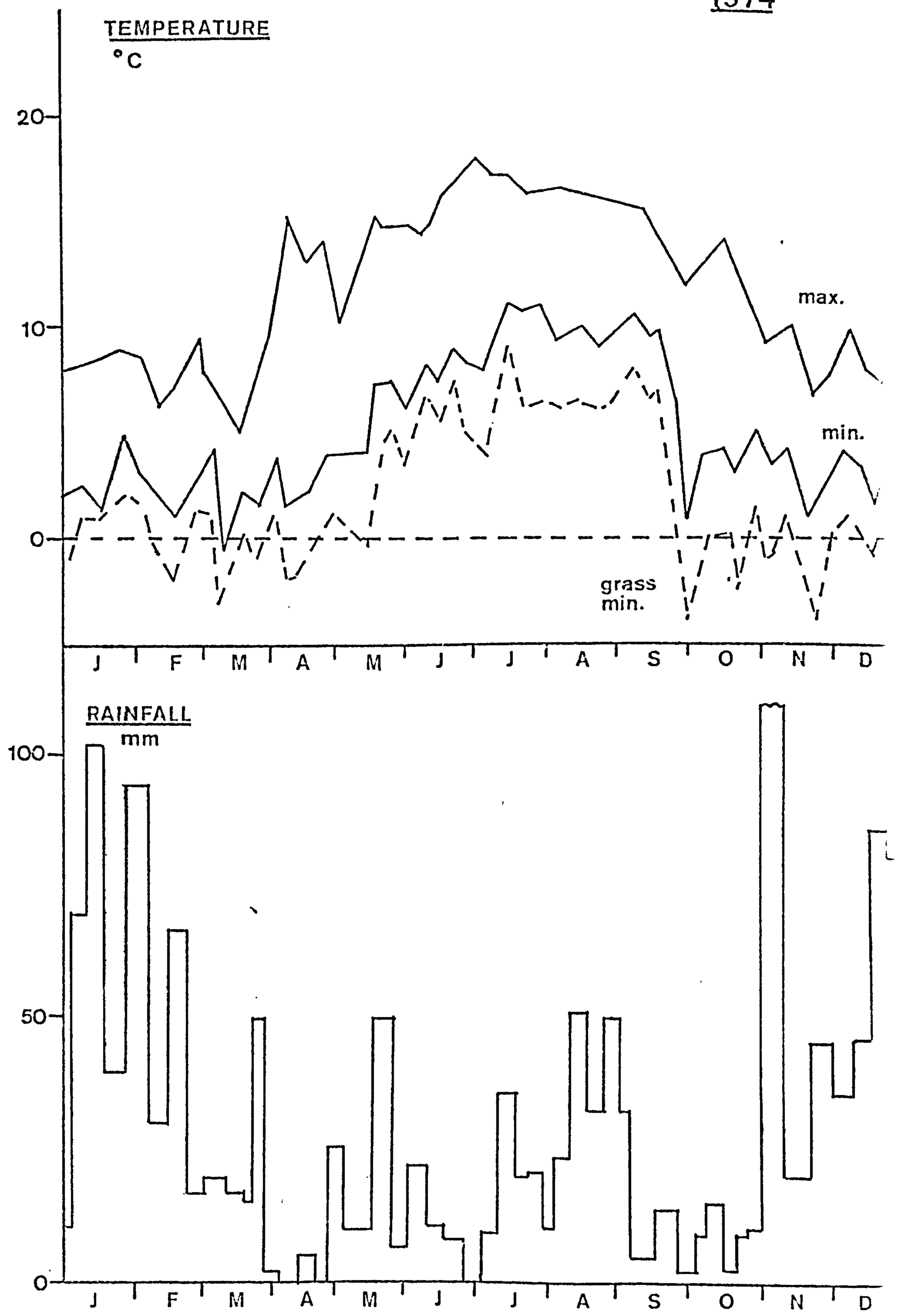
Weather data for Arrochymore, 1973, 1974 and 1975.

(Clyde River Purification Board)

1973


TEMPERATURE
°C
20
10
0
max.
min.
grass
min.
J
F
M
A
M
J
J
A
S
O
N
D
RAINFALL
mm
100
50
0
J
F
M
A
M
J
J
A
S
O
N
D

1974


TEMPERATURE
°C
20
10
0
max.
min.
grass
min.
J
F
M
A
M
J
J
A
S
O
N
D
RAINFALL
mm
100
50
0
J
F
M
A
M
J
J
A
S
O
N
D

1975

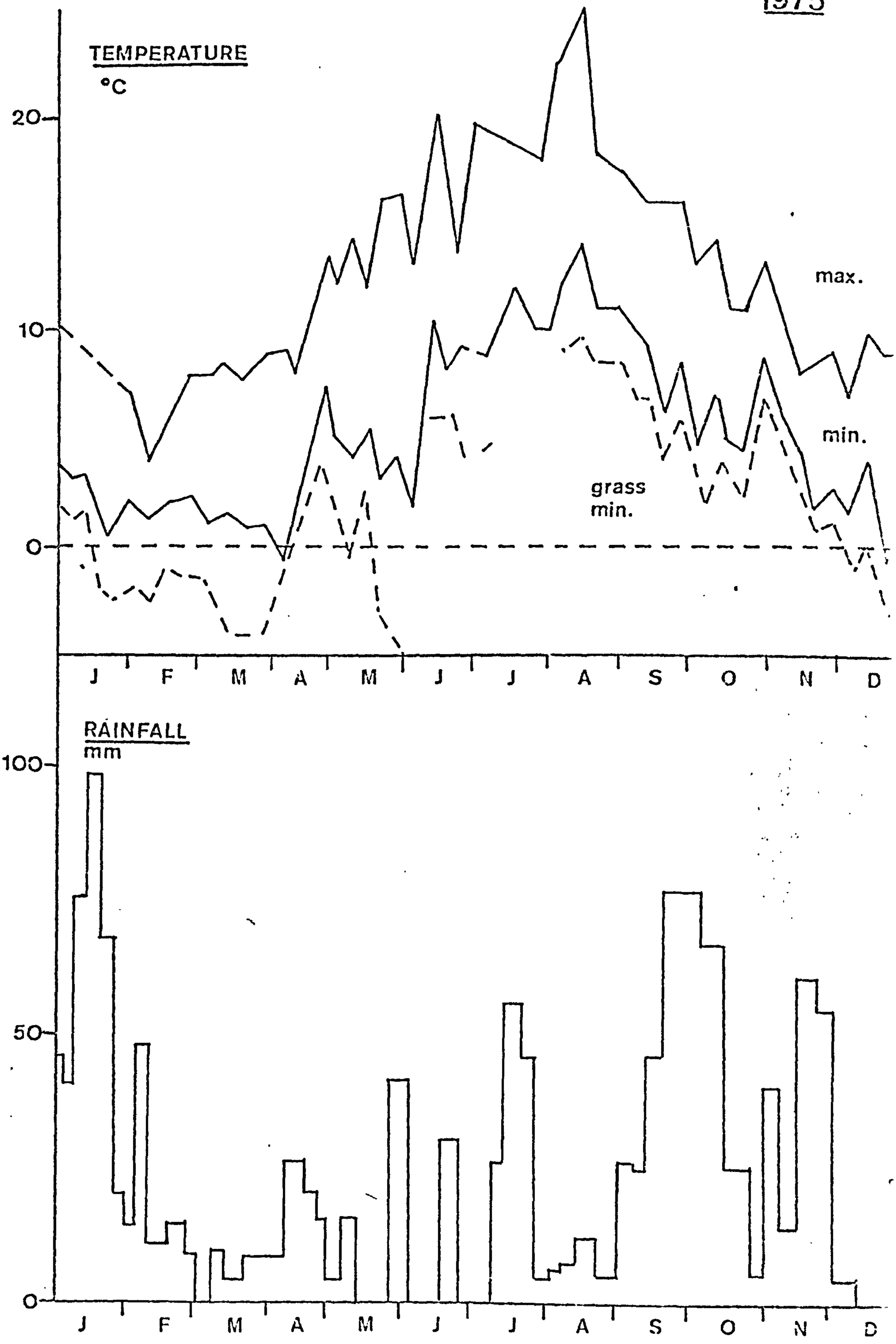

TEMPERATURE
°C
20
10
0
max.
min.
grass
min.
J
F
M
A
M
J
J
A
S
O
N
D
RAINFALL
mm
100
50
0
J
F
M
A
M
J
J
A
S
O
N
D

Table 2:1.

Summary of Weather at Arrochymore - April - June

Mean Temperature (°C)

	1973	1974	1975
Maximum			
April	10.7	13.5	11.3
May	13.0	14.4	14.7
June	17.1	17.2	18.1
April - June	13.66	15.06	14.68
Minimum			
April	2.3	3.1	3.9
May	5.5	5.9	3.7
June	8.4	8.3	8.4
April - June	5.48	5.76	5.30
Grass minimum			
April	- 1.4	- 2.8	0.5
May	3.7	2.69	- 0.96
June	6.1	5.5	5.55
April - June	2.85	2.47	1.40
Total Rainfall (mm)			
April	70.0	22.8	71.4
May	403.4	86.0	23.3
June	117.8	50.4	71.1
April - June	591.8	159.2	166.4

Table 2:2

Summary of Weather at Arrochymore - July - Sept.

Mean Temperature (°C)

	1973	1974	1975
Maximum			
July	19.2	16.6	18.6
Aug.	18.1	17.0	20.8
Sept.	15.6	14.1	14.9
July - Sept.	17.80	15.93	18.13
Minimum			
July	10.4	9.9	11.1
Aug.	10.0	9.7	12.6
Sept.	8.9	7.7	7.5
July - Sept.	9.82	7.87	10.44
Grass minimum			
July	7.8	6.7	-
Aug.	8.9	6.1	9.1
Sept.	5.7	4.3	4.9
July - Sept.	7.51	5.89	7.0
Total Rainfall (mm)			
July	61.3	93.8	126.3
Aug.	169.4	100.3	56.9
Sept.	108.1	171.8	203.6
July - Sept.	277.5	365.9	386.8

Fig. 2:4

Trapping Grid

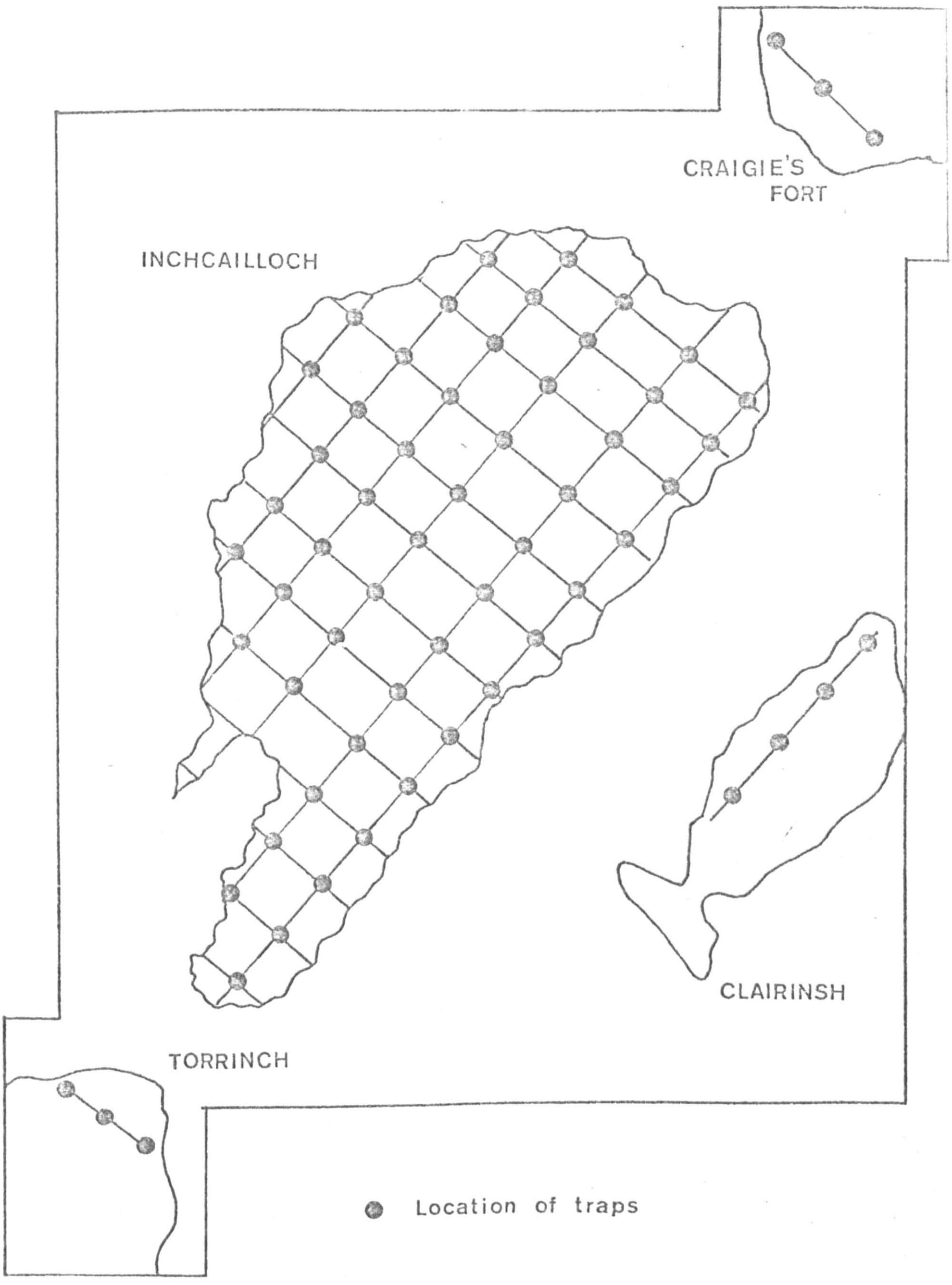

CRAIGIE'S
FORT
INCHCAILLOCH
CLAIRINSH
TORRINCH
Location of traps

Fig. 2:5

Baited trap used for sampling

Traps were inspected once a week. Any beetles trapped were removed and taken to the laboratory to be measured, sexed and marked.

Identification.

Beetles were identified initially using the key in Joy (1932). Nomenclature of Necrophorus, and all other insect species, follows Kloet and Hinks (1945).

Sexing.

Attempts to differentiate the sexes of burying beetles have been made by Horn (1880), Portevin (1926a) and Arnett (1944). The characters used by these workers were the shape of the head, development of the frontal lines of the head, size of the rhinarium and clypeus, appearance of the protarsus and size of the trochanter tooth. These methods were used subsequently by Théorides (1950b), Springett (1967) and Niemitz (1972). Bliss (1949) assessed the reliability of these methods and concluded that no single character was applicable to the whole genus. He further concluded that a combination of the characters listed above could be used with reasonable accuracy to distinguish the sexes of Necrophorus humator and N.investigator, but was unsatisfactory for N.vespilloides. Early in the field study, these conclusions were confirmed, the combined characters proving unreliable for sexing N.vespilloides (Table 2:3).

While examining the beetles, it was noticed that the males have 9 abdominal segments and the females only 8, (fig. 2:6), a difference not mentioned by previous workers. With respect to fig. 2:6, it should be noted that the first abdominal sternite in Coleoptera is not sclerotised, thus there is one more tergite than sternite. There is some disagreement

Table 2:3

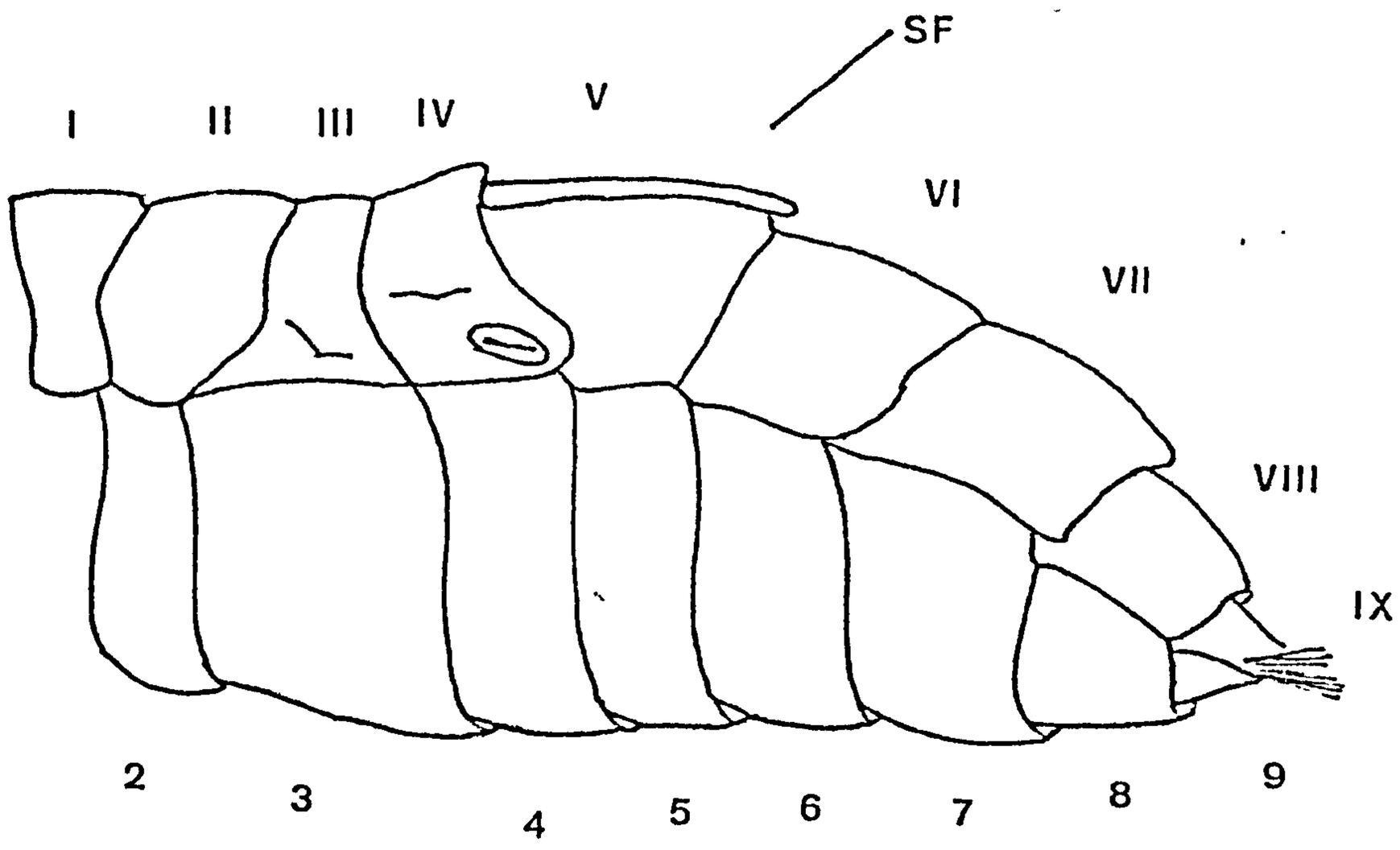
The efficiency of two methods of sexing Necrophorus

Species	1973			1974			1975		
	No. Sexed	No. Incorrect	% Error	No. Sexed	No. Incorrect	% Error	No. Sexed	No. Incorrect	% Error
Bliss's method									
N.vespilloides	516	129	25.00						
N.humator	91	7	7.69	Not used			Not used		
N.investigator	55	3	5.45						
Abdominal method									
N.vespilloides	389	8	2.06	776	6	0.77	521	5	0.96
N.humator	29	1	3.45	35	1	2.86	24	0	0.00
N.investigator	104	3	2.88	43	2	4.65	31	0	0.00

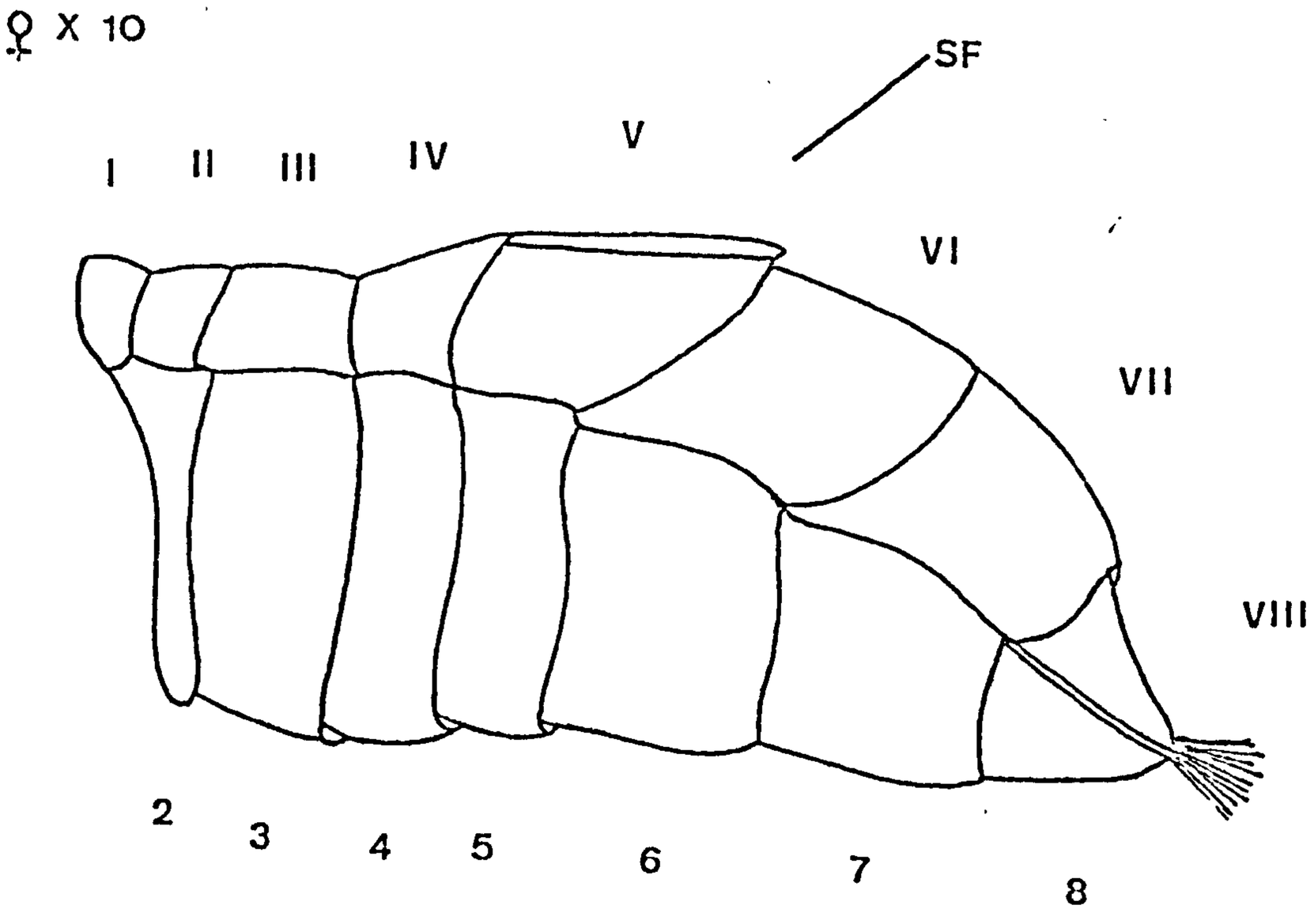
Fig. 2:6

Abdomen of Necrophorus vespilloides, left side, to show the difference between male and female.

♂ X 10



♀ X 10



I-IX : Tergites ; 2-9 : Sternites

SF: Stridulatory Files.

over the number of abdominal segments. Horn (1880) states that Necrophorus has 6 abdominal segments, Bliss (1949) 7 and Niemitz (1972) 10. Crowson (1955) and Schumacher (1973) indicate 8.

The difference in number of segments between male and female appeared to provide a more reliable method of sexing burying beetles than was otherwise available. To test the efficiency of each method, beetles were sexed, during 1973, both by the abdominal method and by Bliss's combined characters and were then dissected to test the accuracy of sexing. There was no significant difference in the reliability of the two methods with respect to N.humator and N.investigator, and the error was less than 10% in each case (Table 2:3). For N.vespilloides the abdominal method was significantly more reliable ($\chi^2 = 92.68$, doff. 1 $p < 0.001$) and the accuracy was greater than 95%. This method therefore was used throughout the rest of the study for all the species.

In 1974 the error in sexing N.vespilloides using the number of abdominal segments was 0.77%, significantly less than in 1973 ($\chi^2 = 6.39$ doff. 1 $p < 0.02$). Therefore the accuracy of sexing improved with practice. This low error was maintained in 1975. There was no significant change in efficiency between the years with respect to N.humator and N.investigator which were less abundant. Thus sexing N.vespilloides, N.humator and N.investigator using the number of abdominal sternites is reliable, and more accurate than other methods. It has the further advantage that with practice, living beetles can be sexed. Examination of specimens in the Bishop Collection, University of Glasgow, suggests that this method may be of use in sexing species of Necrophorus other than those studied.

Measuring:

Beetles were pressed flat and the length from mandible to the tip of the abdomen measured with a ruler. Correlation of length with weight shows that length is a reliable indicator of the size of adult beetles (fig. 2:15).

Marking:

Beetles were marked by mutilation which was considered easier than branding (Springett, 1967). Incisions were made with fine scissors around the edges of the elytra and prothoracic shield. Numbers from 1 to 1,999 could be marked on the beetle (fig. 2:7). No ill effects were apparent after marking and subsequent recapture showed that some marked individuals were long lived.

Release:

Marked beetles were kept in 2 lb Kilner jars containing moist soil and a chick corpse. The beetles were kept in the dark until they were released, two days after capture, at a convenient point on Inchcailloch.

Dissection:

Beetles found dead in the traps were dissected fresh, under water, when the following were noted:

a) Gonads - beetles were classified as immature, mature or post reproductive. The immature category includes callow adults. These were distinguished by the softness of the cuticle, which oozed fluid if cut. In newly emerged individuals, the cuticle is chocolate brown in colour. The other stages are as shown in fig. 2:8. These categories were defined by Springett (1967) who used the term 'spent' rather than post reproductive.

Fig. 2:7

Marking code.

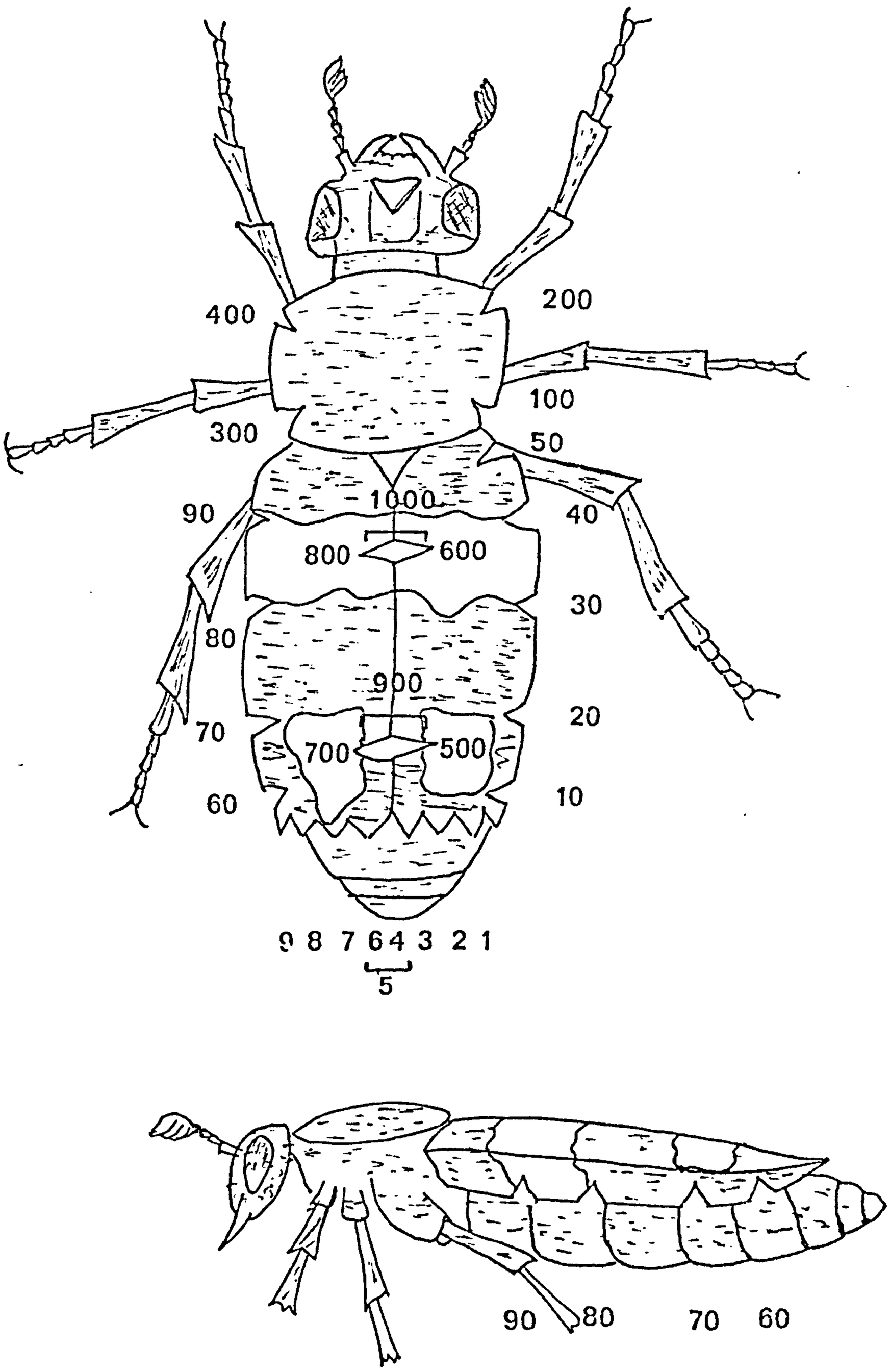
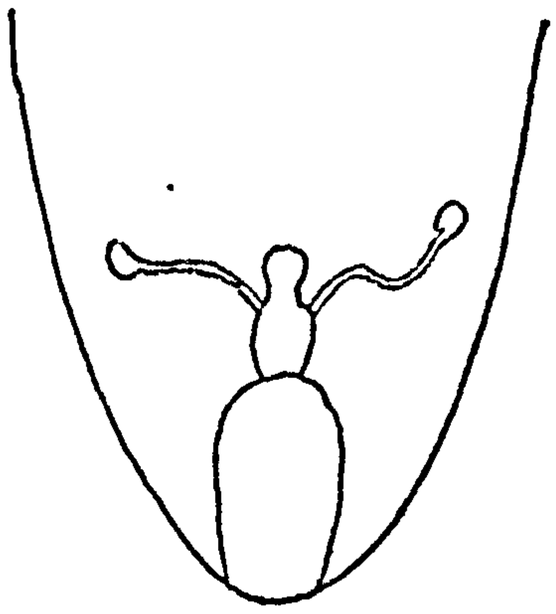
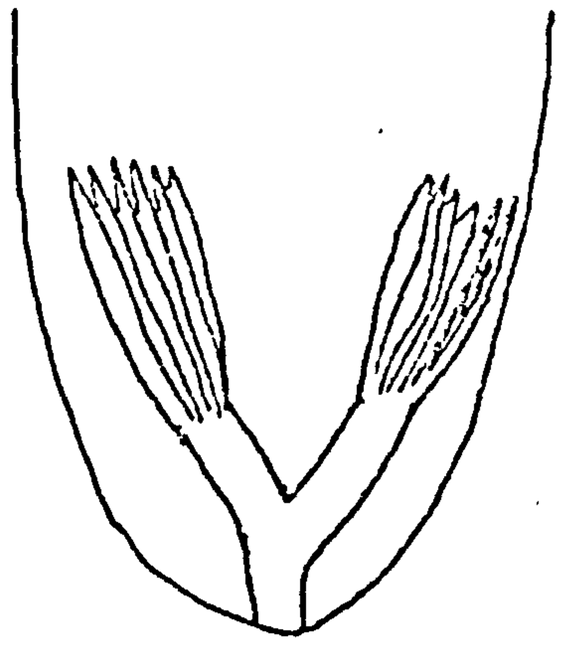
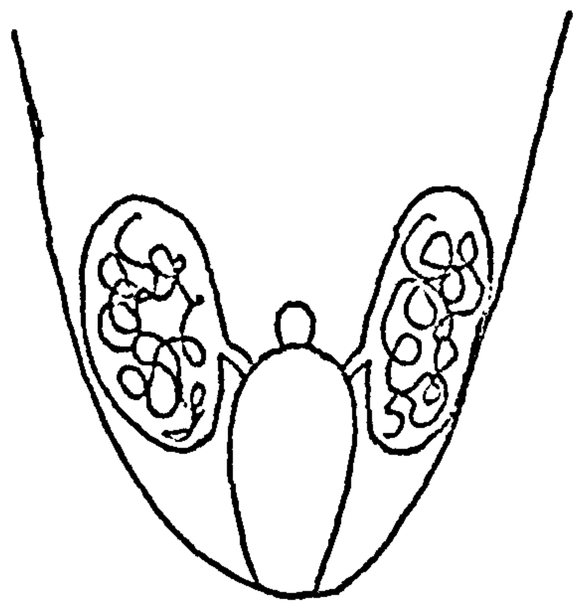
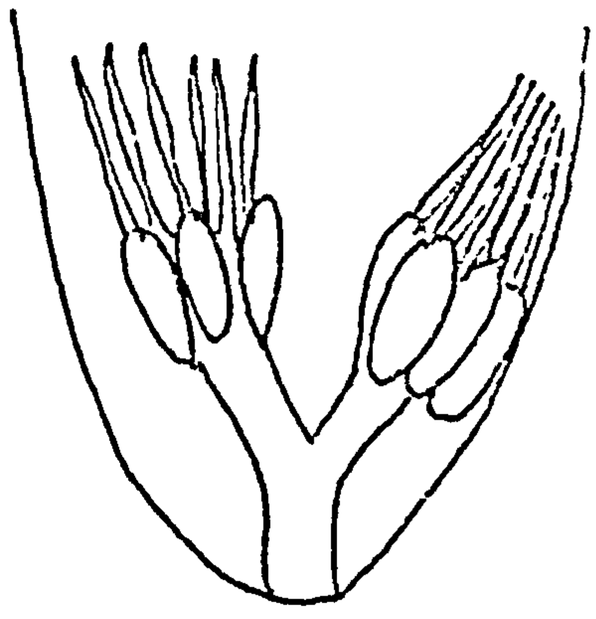
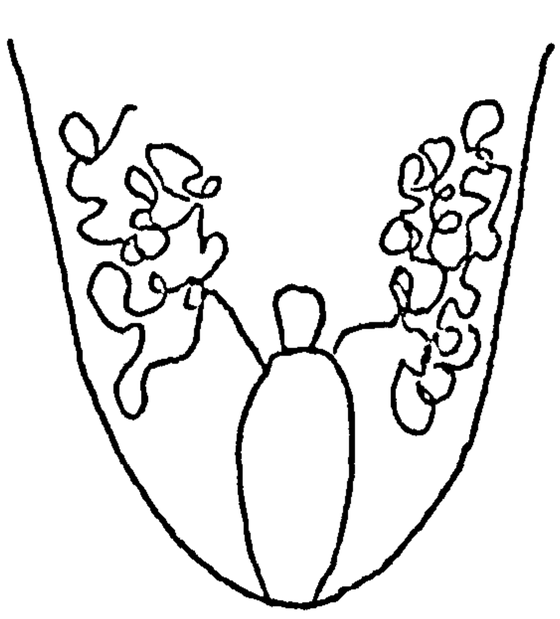
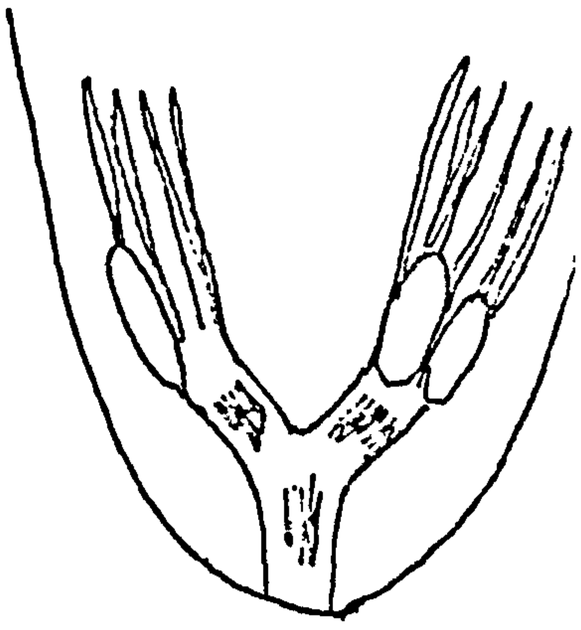

400
200
100
300
50
1000
90
40
800
600
30
80
900
20
70
700
500
10
60
9 8 7 6 4 3 2 1
5
90
80
70
60

Fig. 2:8

Sexual conditions of Necrophorus

	♂	♀
IMMATURE		
	Testes small, undeveloped.	Ovarioles without eggs.
MATURE		
	Testes large, well formed compact.	Pearly white eggs in ovarioles.
POST REPRODUCTIVE		
	Testes diffuse, tangled mass of tubes.	Material in later and common oviducts, eggs present or abser

b) Fat Reserves - the amount of fat in the beetles was assessed on a scale from 0 to 10 (fig. 2:9). Although subjective, this scale gave a comparative assessment of fat body in different individuals. To determine the reliability of this method, fat reserves were measured quantitatively by extraction. A random sample of beetles were weighed, then killed using ethyl acetate. The abdomen was removed, cut open and weighed. The amount of fat was assessed using the subjective scale, and the abdomen was then dried in an oven at 50°C until a constant weight was attained (dryweight). Fat was extracted from the abdomen using a Soxhlet 4 Plls micro extractor. The solvent used was chloroform, and the heating mantle was set at 10°C. An extraction time of twelve hours was found to remove all fat, and this was used in all replicates. After 12 hours extraction, abdomens were returned to the oven for 24 hours and then reweighed. The difference in weight before and after extraction was taken to be due to loss of fat from the abdomen. The size of fat reserve measured in this way was then compared with the subjective estimate.

2.3. Results

2.3.1. Number of beetles trapped.

Three species of burying beetle were found - Necrophorus vespilloides, N.humator and N.investigator. N.vespillo, although found in the general area (Elliot, Laurie and Murdoch, 1901), appears to be restricted to the vicinity of Luss, and has not been recorded from Inchcailloch (R.A. Crowson, pers. comm.).

N.vespilloides was the most numerous species recorded (figs. 2:10 to 2:13). 1981 individuals were trapped in 1973, 1393 in 1974 and 1803 in 1975. N.humator was least numerous with 148 individuals trapped in 1973, 85 in 1974 and 63 in 1975. 299 N.investigator were

Fig. 2:9

Size of fat reserves.

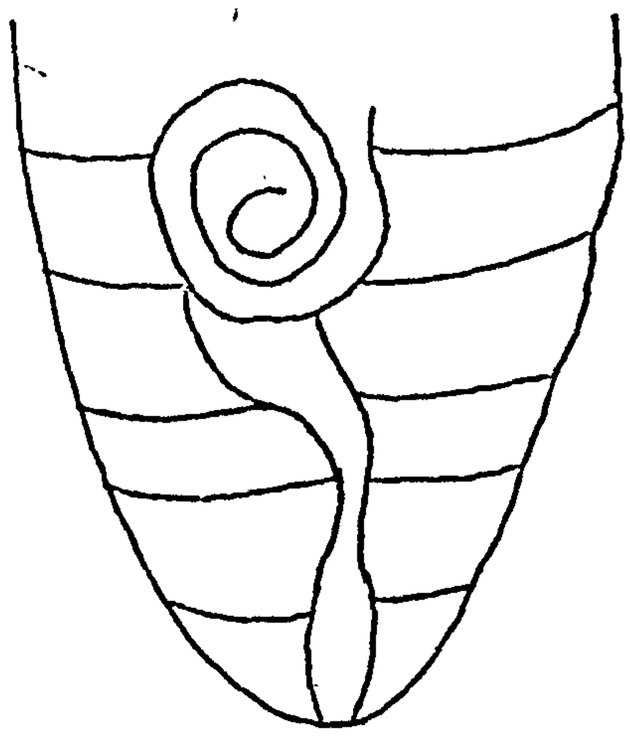
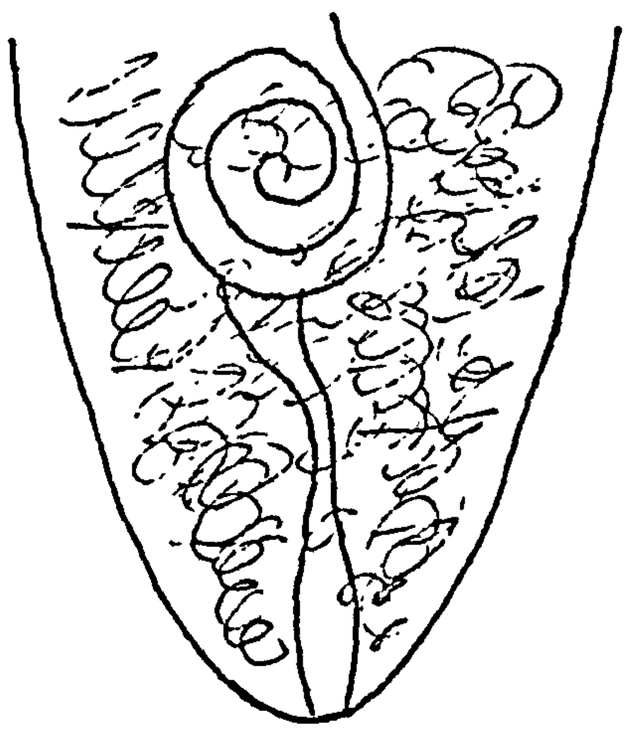
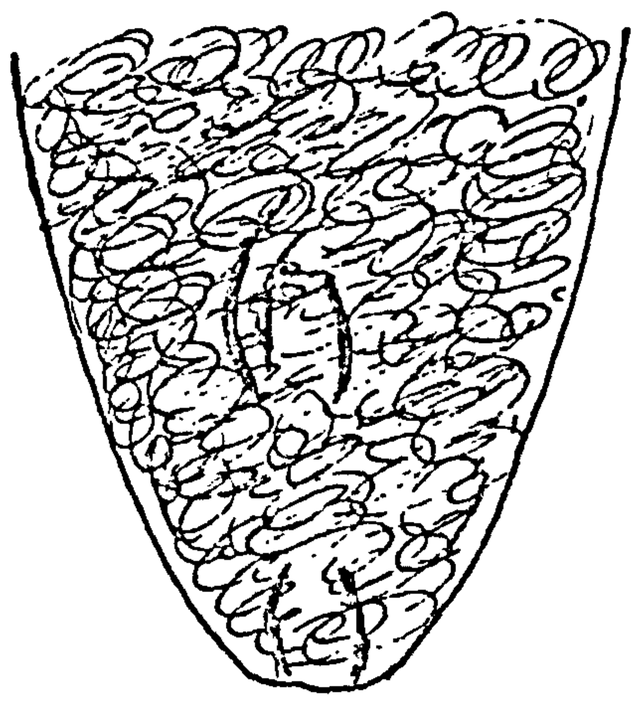
SCALE VALUE		CONDITION
0		No fat in abdomen
5		Fat covers sternites and part of gut
10		Gut and other organs completely covered by fat

Fig. 2:10

Number of Necrophorus trapped on Inchcailloch 1973

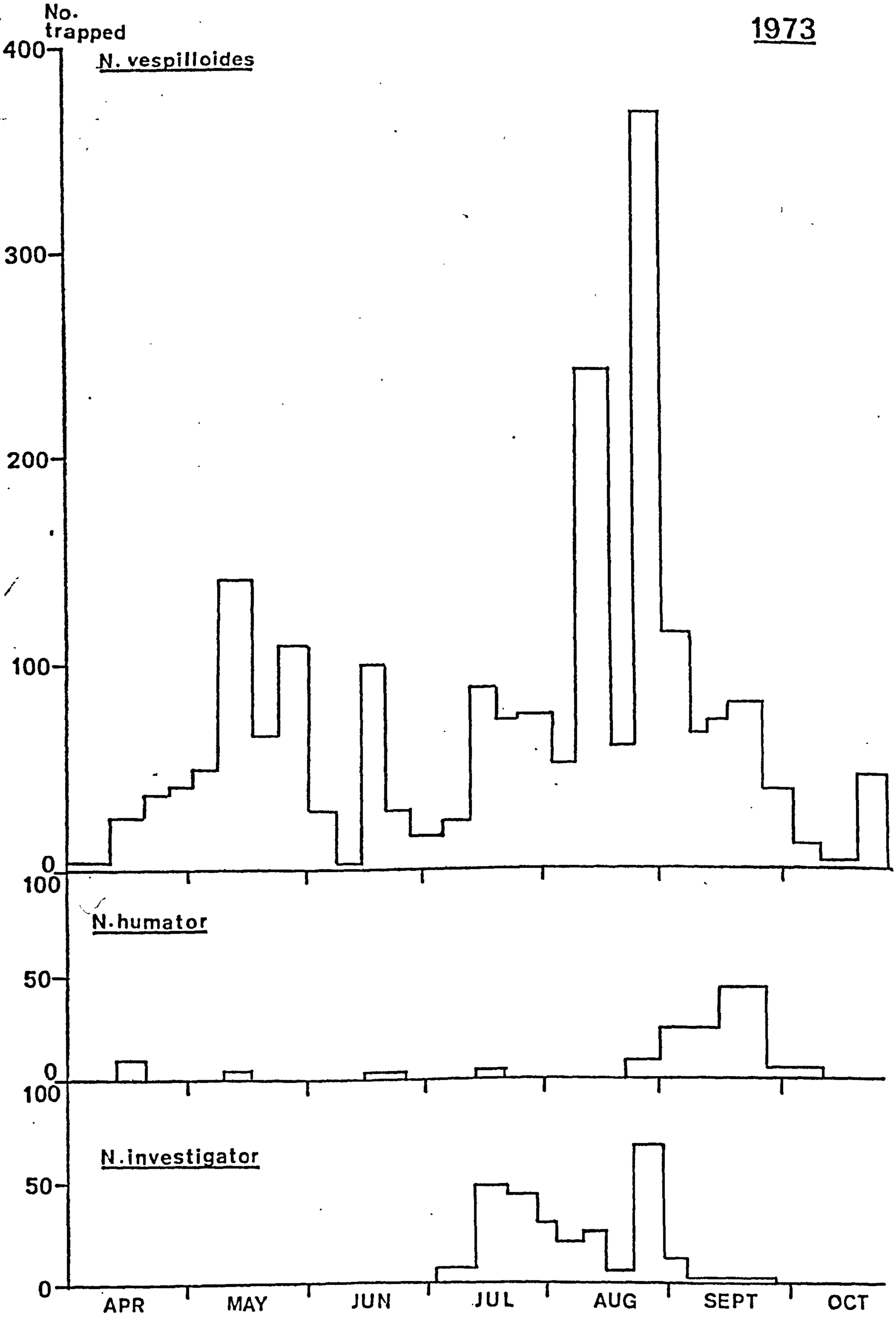

1973
No. trapped
400
300
200
100
0
N. vespilloides
100
0
N.humator
50
0
100
N.investigator
50
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

Fig. 2:11

Number of *Necrophorus* trapped on Inchcailloch 1974

1974

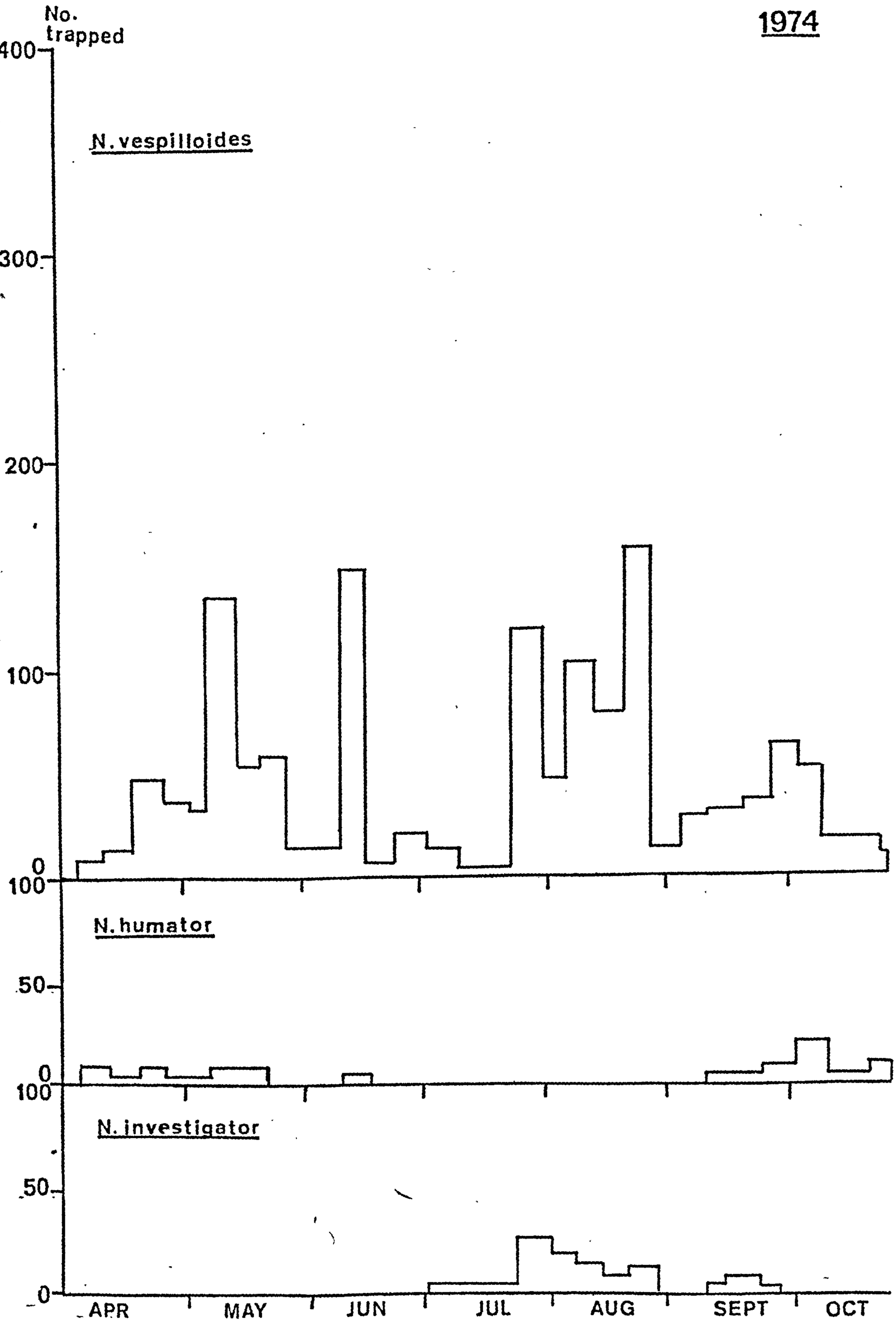

No. trapped
400
N. vespilloides
300
200
100
0
100
N. humator
50
0
100
N. investigator
50
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

Fig. 2:12

Number of Necrophorus trapped on Inchcailloch 1975

1975

No. trapped

N. vespilloides

600
300
200
100
0

N. humator

100
50
0

N. investigator

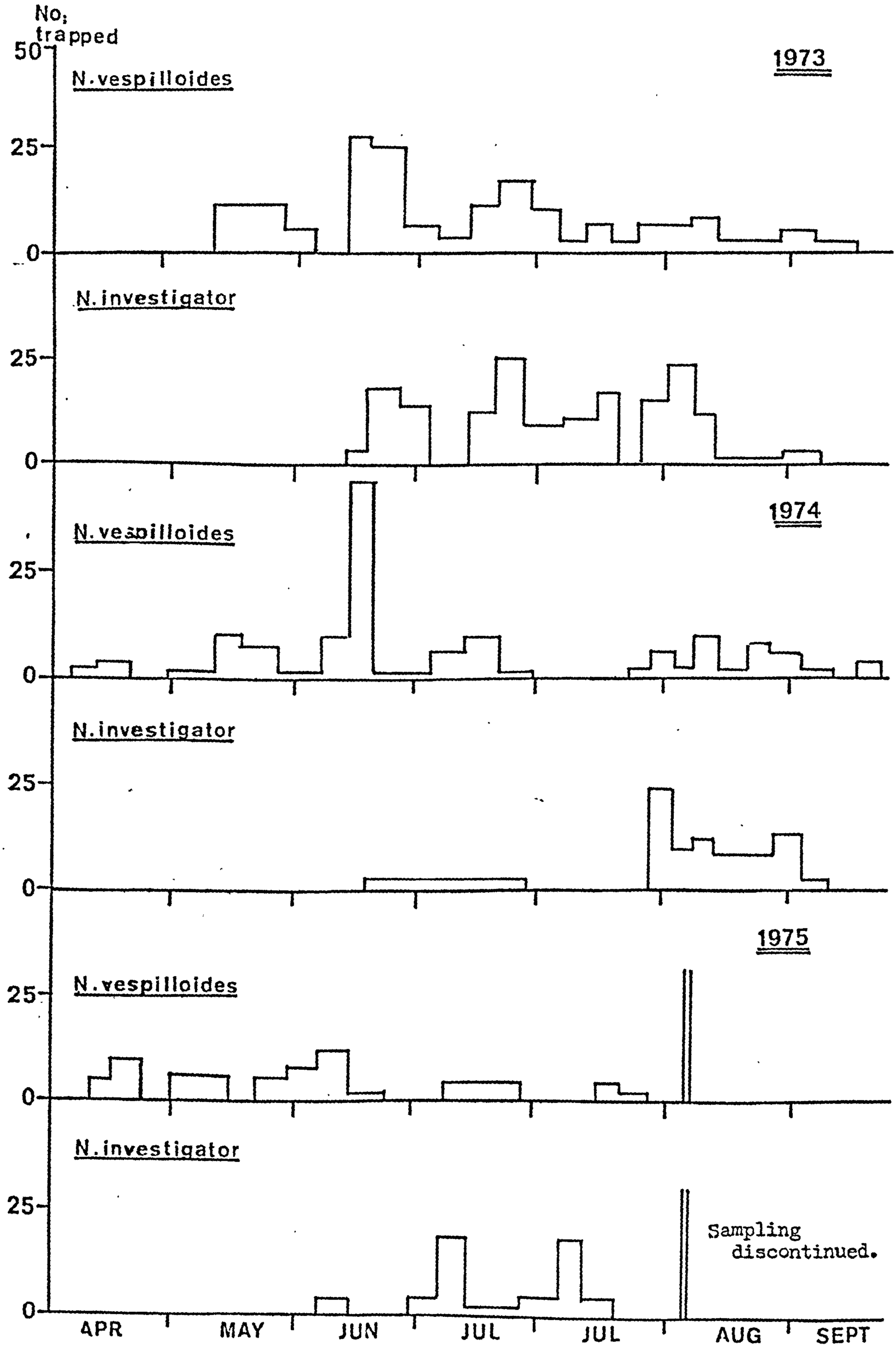
100
50
0

sampling discontinued

APR MAY JUN JUL AUG

Fig. 2:13

Number of Necrophorus trapped on the mainland


No; trapped
50
25
0
N.vespilloides
1973
N.investigator
25
0
N.vespilloides
1974
25
0
N.investigator
25
0
N.vespilloides
1975
25
0
N.investigator
25
0
Sampling discontinued.
APR
MAY
JUN
JUL
JUL
AUG
SEPT

trapped in 1973, 100 in 1974 and 99 in 1975.

N.vespilloides was recorded on Inchcailloch from April until November. Individuals were first trapped on 12 April, 1973, 24 April, 1974 and 18 April 1975. The earlier emergence of N.vespilloides in 1974 may be due to the warm conditions at the beginning of April in that year (fig. 2:3). Two peaks in numbers occur each year, the first sometime in April, May or June and the second in July, August or September. The size of the second peak varied greatly from year to year, that observed in 1975 being the highest and that in 1974 the smallest. N.vespilloides was last trapped on Inchcailloch on 8 November, 1973 and 18 November 1974.

The number of N.vespilloides trapped on Clairinsh and Torrinch was lower than on Inchcailloch, and is not shown on the graphs. The same variation within and between years occurred on these islands as on Inchcailloch.

Overall, fewer N.vespilloides were trapped on the mainland than on Inchcailloch. However, there were fewer traps on the mainland and there was no significant difference in the mean number of beetles caught per trap in the two areas (Table 2:4). Therefore, N.vespilloides is caught at the same rate on the mainland as it is on Inchcailloch. Although the actual number of beetles trapped is smaller than that on Inchcailloch, a spring peak can be identified each year on the mainland as on the islands (fig. 2:13). However, no late summer peak, as observed on Inchcailloch, Torrinch and Clairinsh, was recorded on the mainland in any of the three years of the study.

N.humator was trapped from April until November. It is possible that it too shows two peaks in abundance but too few individuals

Table 2:4

Mean number of beetles caught per trap on Inchcailloch and the mainland.

	$\bar{x}$ beetles/trap				
	Inchcailloch	Mainland	t	doff	p
N.vespilloides					
1973	38.67	52.67	0.856	52	> 0.05
1974	27.90	38.67	0.973	51	> 0.05
1975	37.43	17.33	1.421	49	> 0.05
N.humator					
1973	2.72	51.0	20.026	52	< 0.001
1974	1.32	28.00	6.074	51	< 0.001
1975	1.67	18.33	11.871	49	< 0.001
N.investigator					
1973	5.62	54.33	12.140	52	< 0.001
1974	2.20	23.67	9.647	51	< 0.001
1975	2.06	15.00	3.747	49	< 0.001

were trapped to make this clear. Although not shown on fig. 2:13, the distribution of abundance on the mainland is also similar to that of N.vespilloides, and no late summer peak was observed. The mean number of N.humator per trap on the mainland is significantly different from the mean number caught per trap on Inchcailloch. This suggests that N.humator may be more abundant on the mainland than on Inchcailloch.

N.investigator was recorded from July until October, and only one peak in numbers was observed. More beetles were trapped on Inchcailloch and the mainland in 1973 than in 1974 and 1975. N.investigator was first recorded on Inchcailloch on 5 July 1973, 12 July 1974 and 3 July 1975. Beetles were trapped significantly earlier than this on the mainland (Table 2:5) and N.investigator was present from June until October. In 1975, several N.investigator were found on the Ross Point in May. The average number of beetles caught in each trap on the mainland is significantly different from that on Inchcailloch (Table 2:4), suggesting that N.investigator may be more numerous on the mainland.

2.3.2. Size of beetles.

N.humator is the largest of the three species, being about 2.3cm in length, and N.vespilloides is the smalles at 1.6cm (fig. 2:14). N.investigator measures about 1.9cm. There is no significant difference between the sexes in any of the species. Size is normally distributed within the population.

To test the reliability of length as an indicator of size, a number of beetles were weighed after being measured. In all cases there was a significant correlation between body length and live weight (fig. 2:15). Therefore length is a good estimate of body size. It is

Table 2:5

Date of earliest trapping of N.investigator

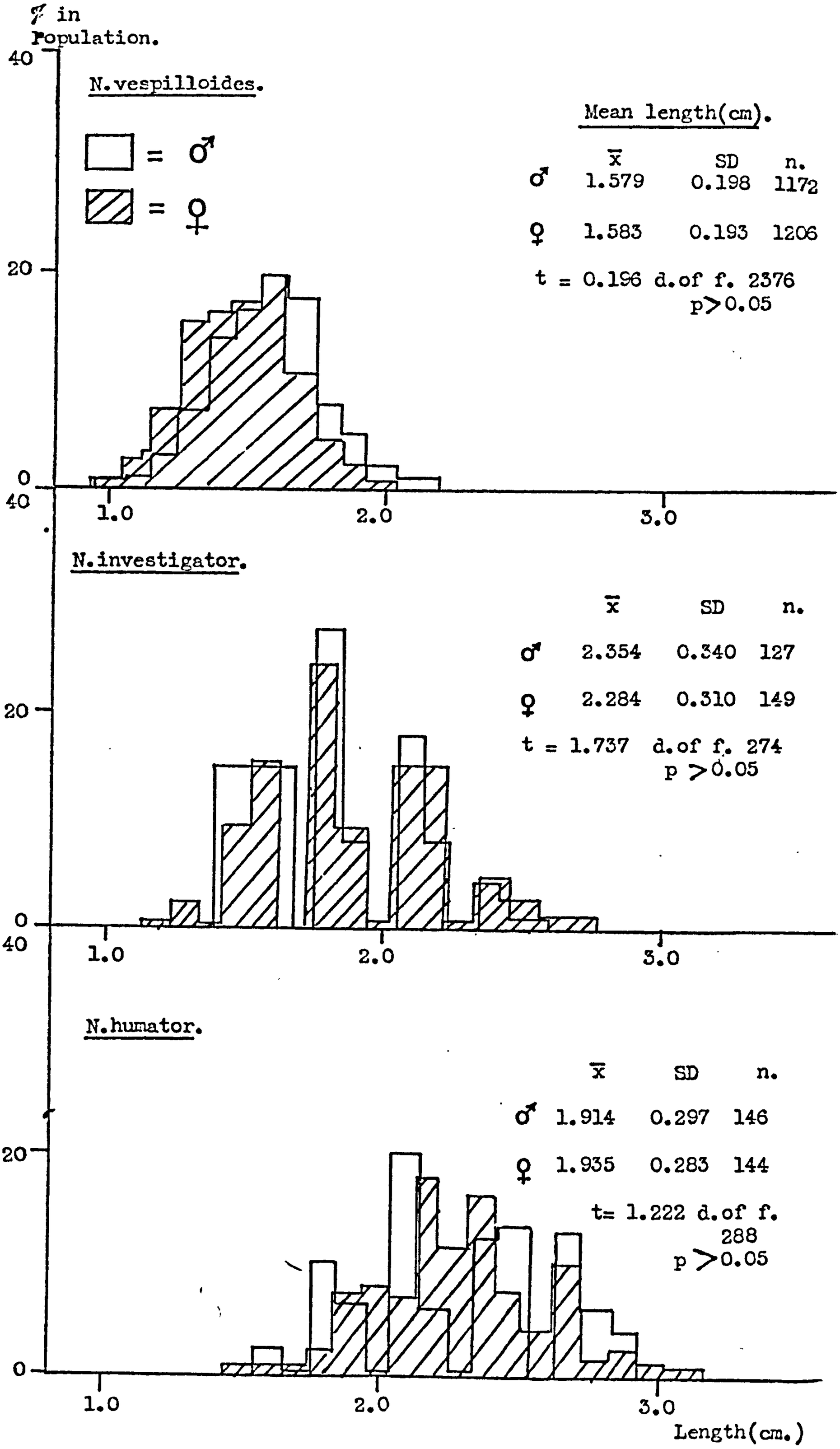
Year	Inchcailloch		Mainland	
	Date of Emergence	Week number (from 1st Jan.)	Date of Emergence	Week number (from 1st Jan.)
1973	5th July	28	1st June	23
1974	12th July	28	20th June	25
1975	3rd July	27	13th June	24 *

Difference in emergence times between Inchcailloch and the mainland significant at $p = 0.05$ (Mann Whitney U test)

* Note N.investigator found in May 1975 at Ross Point.

Fig. 2:14

Distribution of sizes in the population



Mean length(cm).

	$\bar{x}$	SD	n.
♂	1.579	0.198	1172
♀	1.583	0.193	1206

t = 0.196 d.of f. 2376
p > 0.05

	$\bar{x}$	SD	n.
♂	2.354	0.340	127
♀	2.284	0.310	149

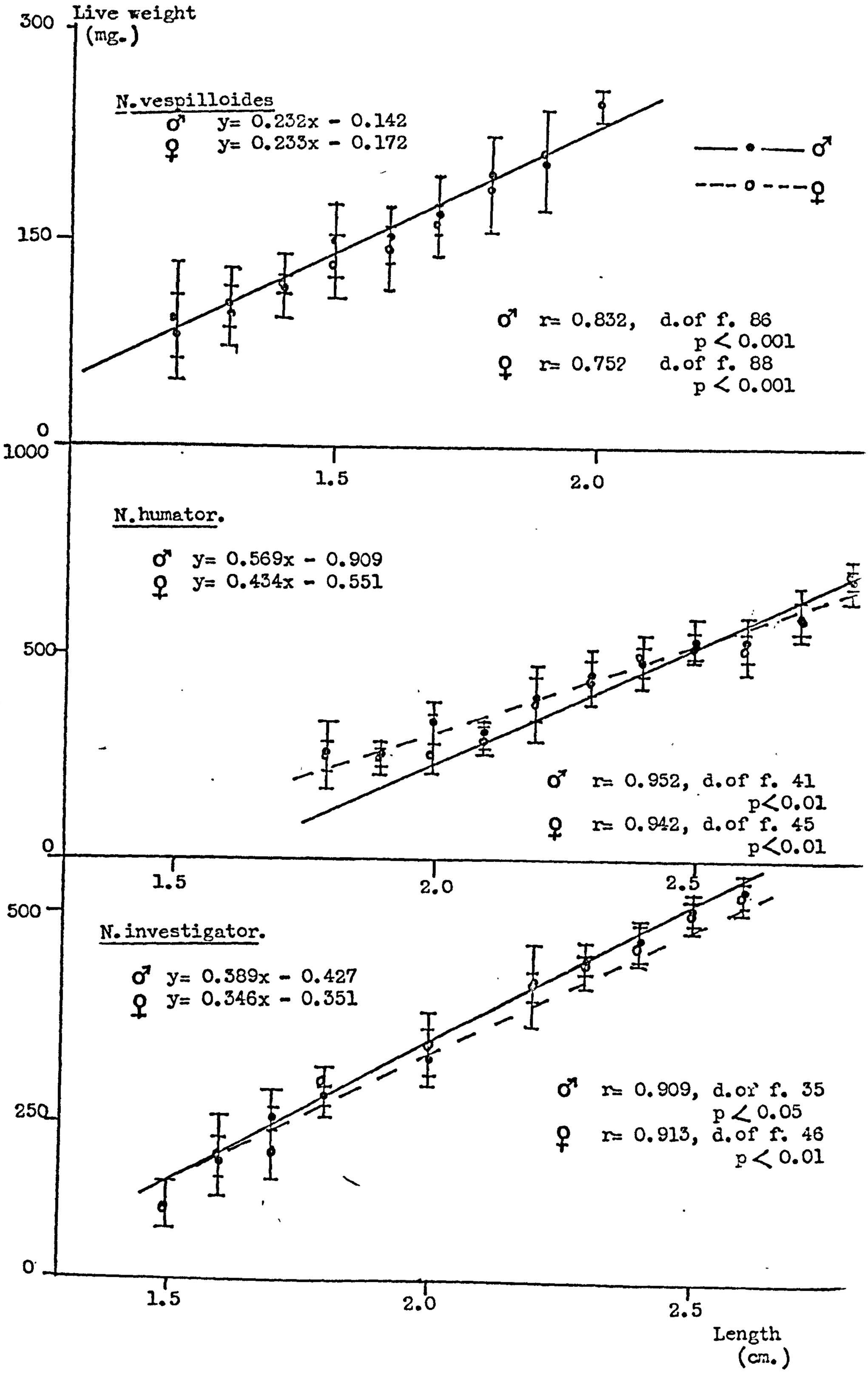
t = 1.737 d.of f. 274
p > 0.05

	$\bar{x}$	SD	n.
♂	1.914	0.297	146
♀	1.935	0.283	144

t= 1.222 d.of f. 288
p > 0.05

Fig. 2:15

Length/weight relationships of Necrophorus. Each point is the mean of weight data for each size class, and the bar represents standard deviation. Correlations were performed using all data.


300
Live weight
(mg.)
N.vespilloides
♂ y= 0.232x - 0.142
♀ y= 0.233x - 0.172
♂
♀
150
♂ r= 0.832, d.of f. 86
p < 0.001
♀ r= 0.752 d.of f. 88
p < 0.001
0
1000
1.5
2.0
N.humator.
♂ y= 0.569x - 0.909
♀ y= 0.434x - 0.551
500
♂ r= 0.952, d.of f. 41
p<0.01
♀ r= 0.942, d.of f. 45
p<0.01
0
1.5
2.0
2.5
500
N.investigator.
♂ y= 0.389x - 0.427
♀ y= 0.346x - 0.351
♂ r= 0.909, d.or f. 35
p < 0.05
♀ r= 0.913, d.of f. 46
p < 0.01
250
0
1.5
2.0
2.5
Length
(cm.)

moreover, quicker than weighing and can be used in the field. No attempt was made to estimate the weight of a beetle from its length, as proposed by Rogers, Hinds and Buchsbom (1976).

2.3.3. Sex Ratio.

In 1973, a significantly higher proportion of male than female N.vespilloides was trapped (Table 2:6). The proportion of male and female N.vespilloides trapped was the same in 1974 and 1975, and in all three years for N.humator and N.investigator. Despite weekly variation, the sex ratio of N.vespilloides was significantly different from a ratio of 1:1 only three times in 1973 (fig. 2:16). However, consideration of fig. 2:16 suggests that slightly more males were caught from April until August 1973 and 1974 (April to June 1975), and thereafter similar proportions of males and females are caught. The slightly higher proportion of males earlier in the year may be due to the absence of some females underground during breeding. Without knowledge of the sex ratios in the population, however, it is only possible to conclude that the sex ratio of trapped beetles was normally 1:1. The number of N.humator and N.investigator trapped each week was too low to show any trends in sex ratio (figs. 2:17, 2:18).

2.3.4. Selection of areas within the island.

The rocks on either side of the Highland Boundary Fault are different (fig. 2:2) and these differences are reflected in the soils and flora. Williamson (1972) has shown corresponding differences in the breeding bird communities, with more breeding pairs on the west side of the Highland Boundary Fault than on the east. In 1973 and 1974, more N.vespilloides were found on the west than east side of Inchcailloch (Table 2:7). Therefore in both these years differences in habitat were

Table 2:6

Sex ratios of Necrophorus trapped on Inchcailloch

Year	Total number sexed	Male No.	Male %	Female No.	Female %	Difference from 50:50 χ^2	doff	p
N.vespilloides								
1973	1701	1102	64.78	599	35.21	25.18	1	$<$ 0.001
1974	1453	720	49.55	733	50.54	0.058	1	$>$ 0.05
1975	1728	824	47.69	904	52.31	1.853	1	$>$ 0.05
N.humator								
1973	118	64	54.24	54	45.76	0.424	1	$>$ 0.05
1974	163	69	42.33	94	57.67	1.928	1	$>$ 0.05
1975	107	48	44.86	59	55.14	0.507	1	$>$ 0.05
N.investigator								
1973	149	76	51.01	73	48.99	0.030	1	$>$ 0.05
1974	159	77	48.43	82	51.57	0.079	1	$>$ 0.05
1975	137	70	51.09	67	48.91	0.033	1	$>$ 0.05

Fig. 2:16

Sex ratios of Necrophorus vespilloides trapped on Inchcailloch

\+ = number of individuals less than 10

* = sex ratio significantly different from 50:50 ratio at p = 0.05.

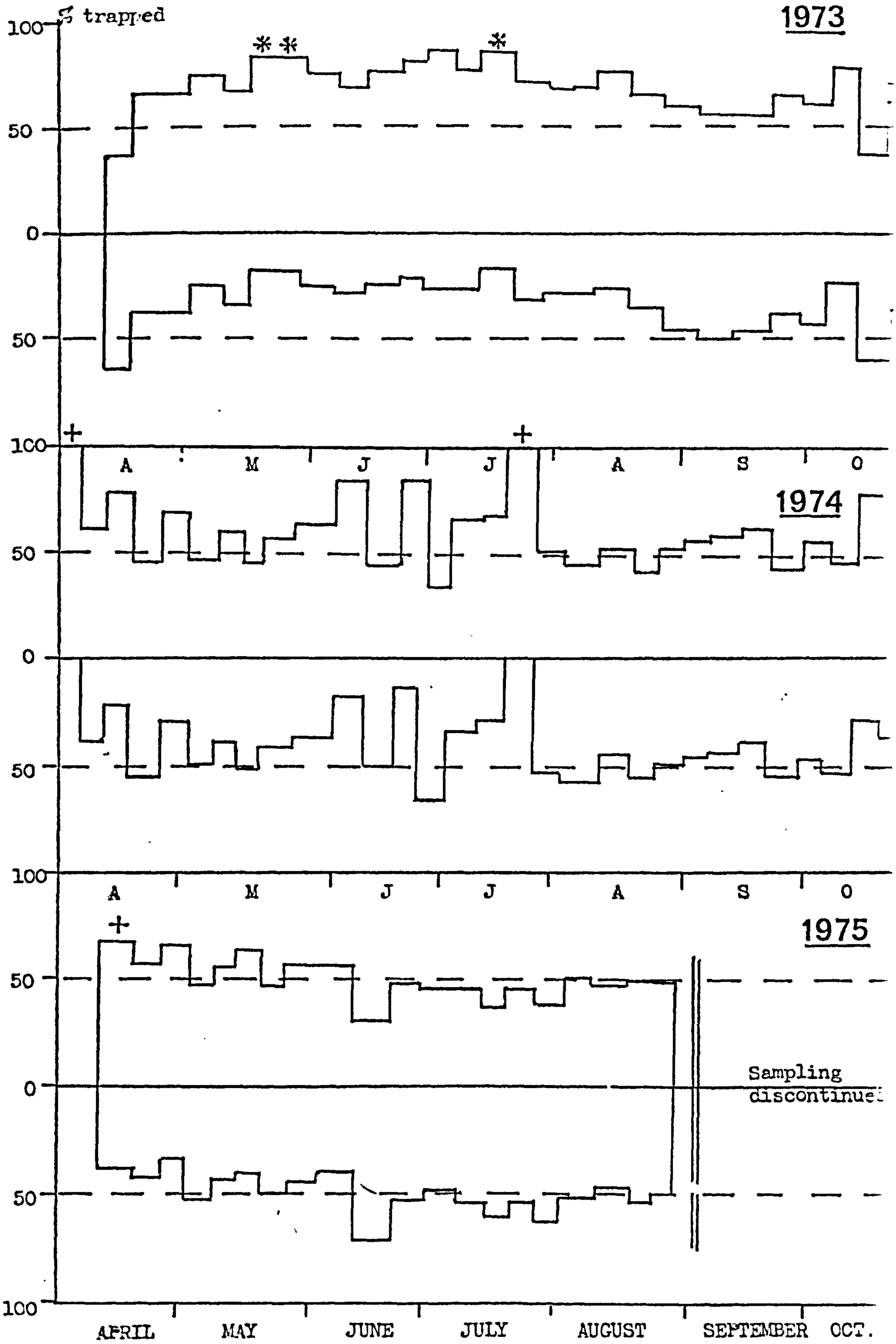

% trapped
1973
100
50
0
* *
*
100
50
A
M
J
J
A
S
O
1974
0
50
100
A
M
J
J
A
S
O
1975
50
0
50
100
Sampling discontinued
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCT.

Fig. 2:17

Sex ratios of Necrophorus humator trapped on Inchcailloch

Symbols as for fig. 2:16.

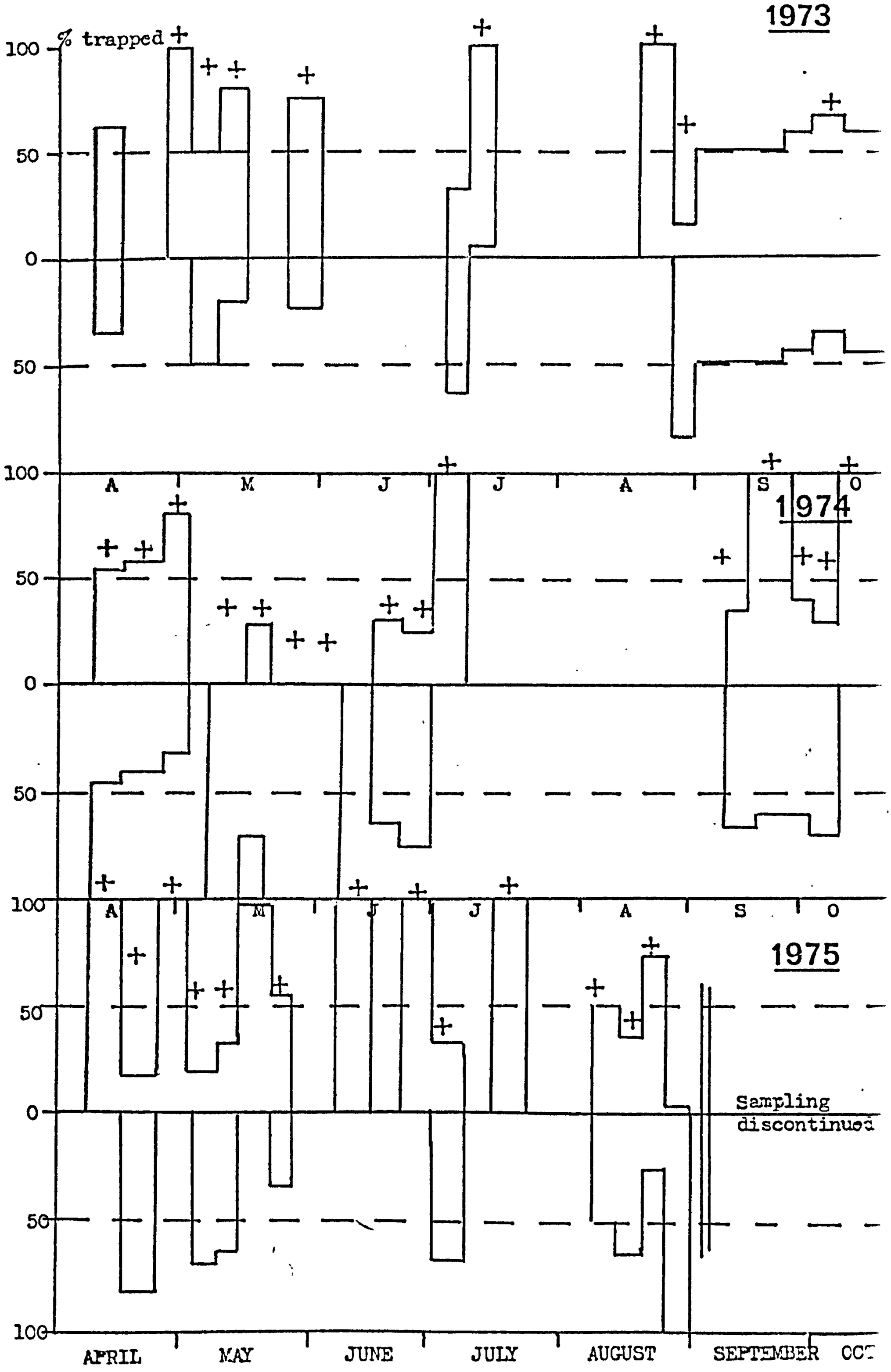

1973
% trapped
100
50
0
50
A
M
J
J
A
S
O
1974
100
50
0
50
100
A
M
J
J
A
S
O
1975
Sampling discontinued
100
50
0
50
100
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCT

Fig. 2:18

Sex ratios of Necrophorus investigator trapped on Inchcailloch

Symbols as for fig. 2:17

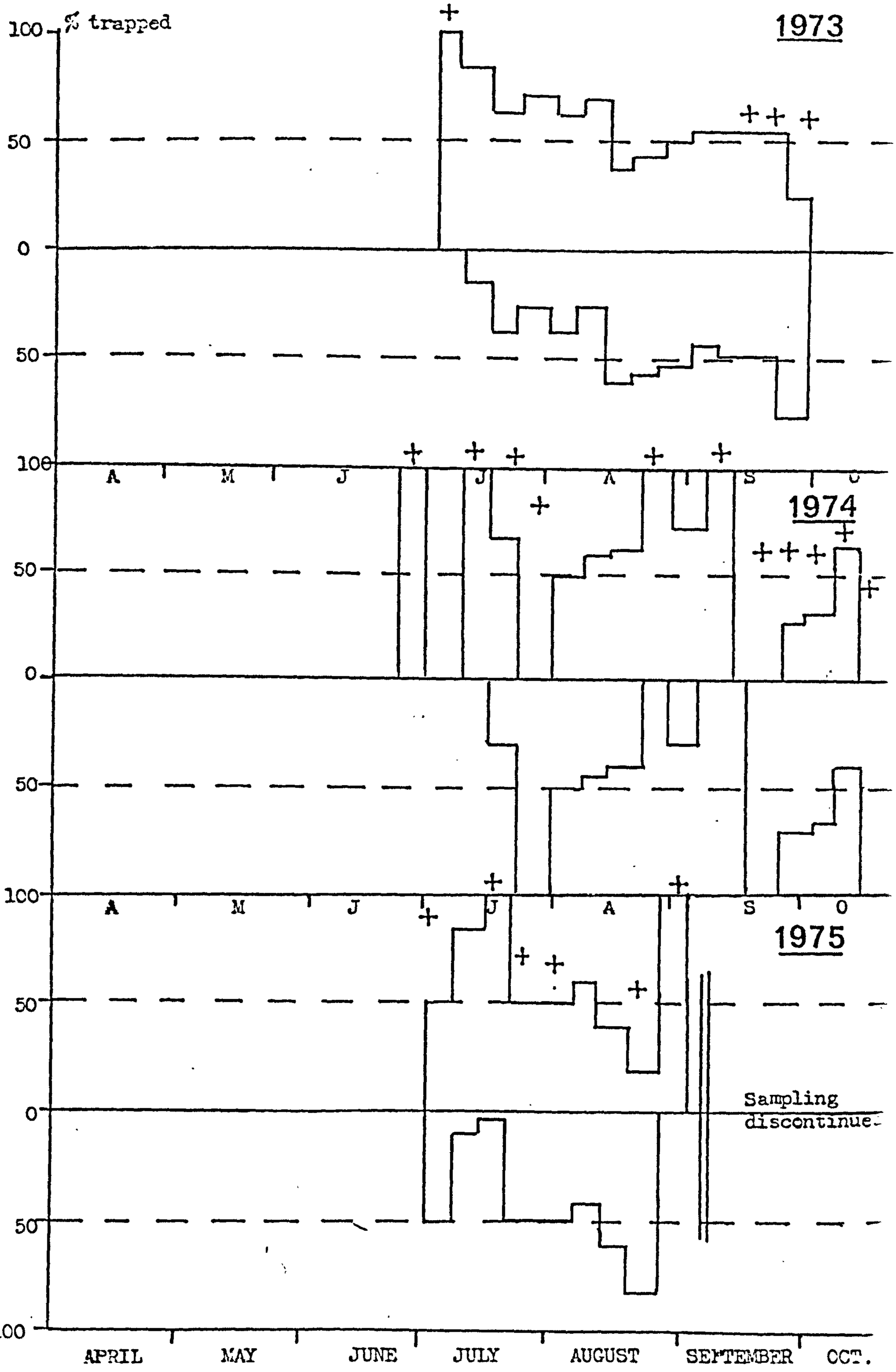

100
% trapped
1973
50
0
50
100
A
M
J
J
A
S
O
1974
50
0
50
100
A
M
J
J
A
S
O
1975
50
0
Sampling discontinue-
50
100
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCT.

Table 2:7

Comparison of Necrophorus trapped on either side of the Highland Boundary Fault

Year	Number beetles trapped on Inchcailloch West* (No. traps = 26)	Number beetles trapped on Inchcailloch East* (No. traps = 25)	Comparison with ratio of 50:50 χ^2	doff	p
N.vespilloides					
1973	1102	835	18.940	1	< 0.001
1974	775	620	8.638	1	< 0.01
1975	891	906	0.067	1	> 0.05
N.humator					
1973	84	64	1.357	1	> 0.05
1974	46	36	0.612	1	> 0.05
1975	40	22	2.669	1	> 0.05
N.investigator					
1973	132	160	1.345	1	> 0.05
1974	59	52	0.221	1	> 0.05
1975	49	50	0.005	1	> 0.05

* These are the same as the areas defined by Williamson (1972).

reflected in differences in density of burying beetles. This was not observed for N.vespilloides in 1975, or for N.humator or N.investigator which appeared to be present in equal densities on both sides of the Highland Boundary Fault.

2.3.5. Sexual Condition.

The proportions of N.vespilloides and N.investigator identifed by dissection as immature, mature and post reproductive is shown in figs. 2:19 to 2:24. Too few N.humator were dissected for any conclusions to be reached for this species.

Two generations of immature N.vespilloides occur each year. Sexually immature second generation individuals are at first callow and appeared initially on 18 July 1973, 12 July 1974 and 5 July 1975. Immature beetles taken later in these years were classed as second generation individuals. This would be inaccurate if immature first generation adults survive until then. Only one generation of N.investigator can be observed each year. This may be related to the observed distribution of number of beetles trapped (fig. 2:11 to 2:21 and 2:10 to 2:12). For N.vespilloides, the first peak consists of immature first generation, mature and post reproductive individuals, and the second peak of immature second generation adults. The population of N.investigator consists of immature, mature and post reproductive adults in a single peak.

There is a slight delay between the appearance of immature first generation N.vespilloides and of mature adults (figs. 2:19 to 2:21). This may be associated with the time taken to mature gonads by feeding, which Springett (1967) suggests is about 14 days for N.humator. Mature adults of N.vespilloides were present from mid April until mid September

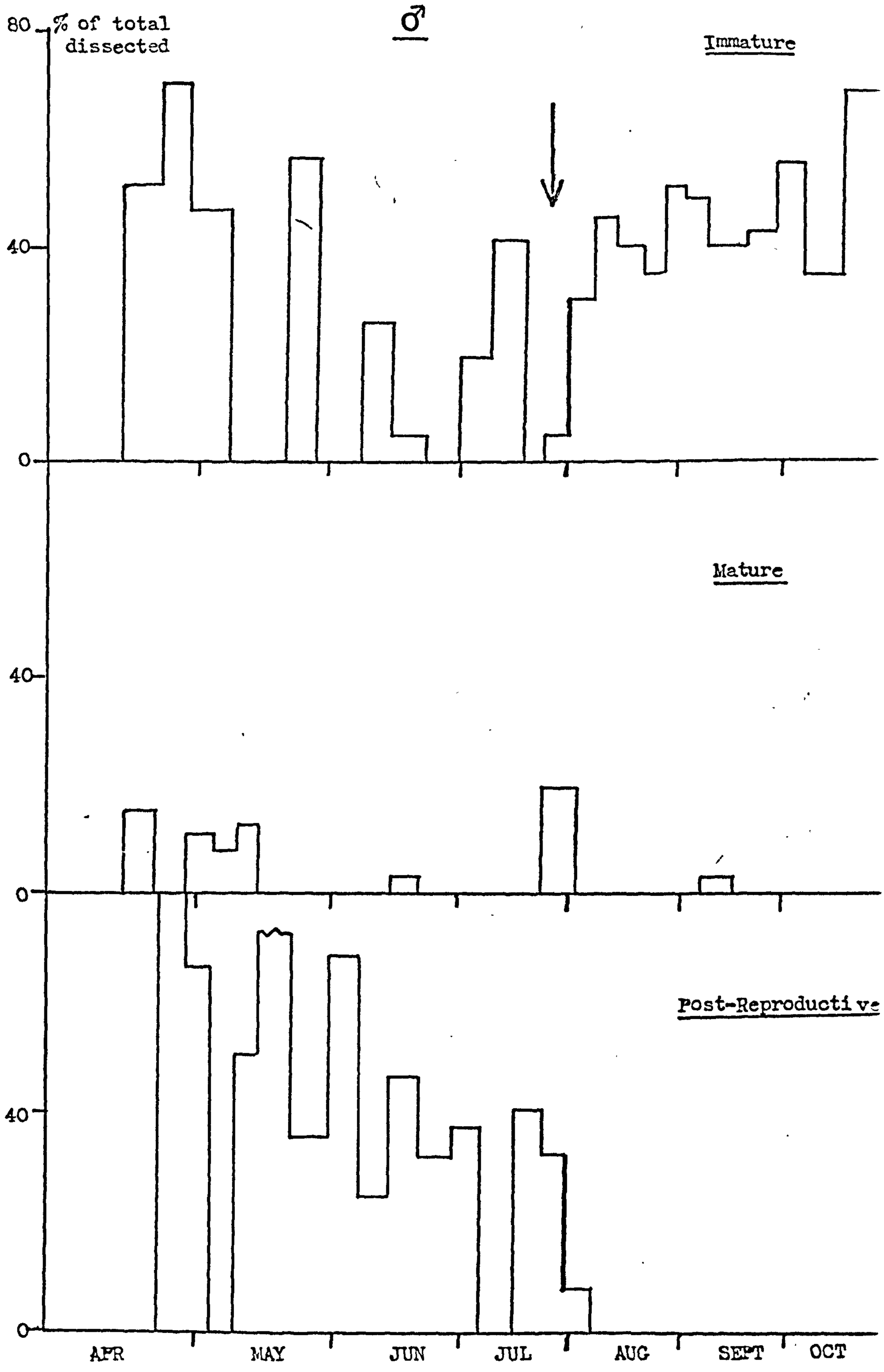
Fig. 2:19

Sexual condition of Necrophorus vespilloides 1973

↓ = first emergence of 2nd generation immature

A = ♂

B = ♀


♂
Immature
80
% of total
dissected
40
0
Mature
40
0
Post-Reproductive
40
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

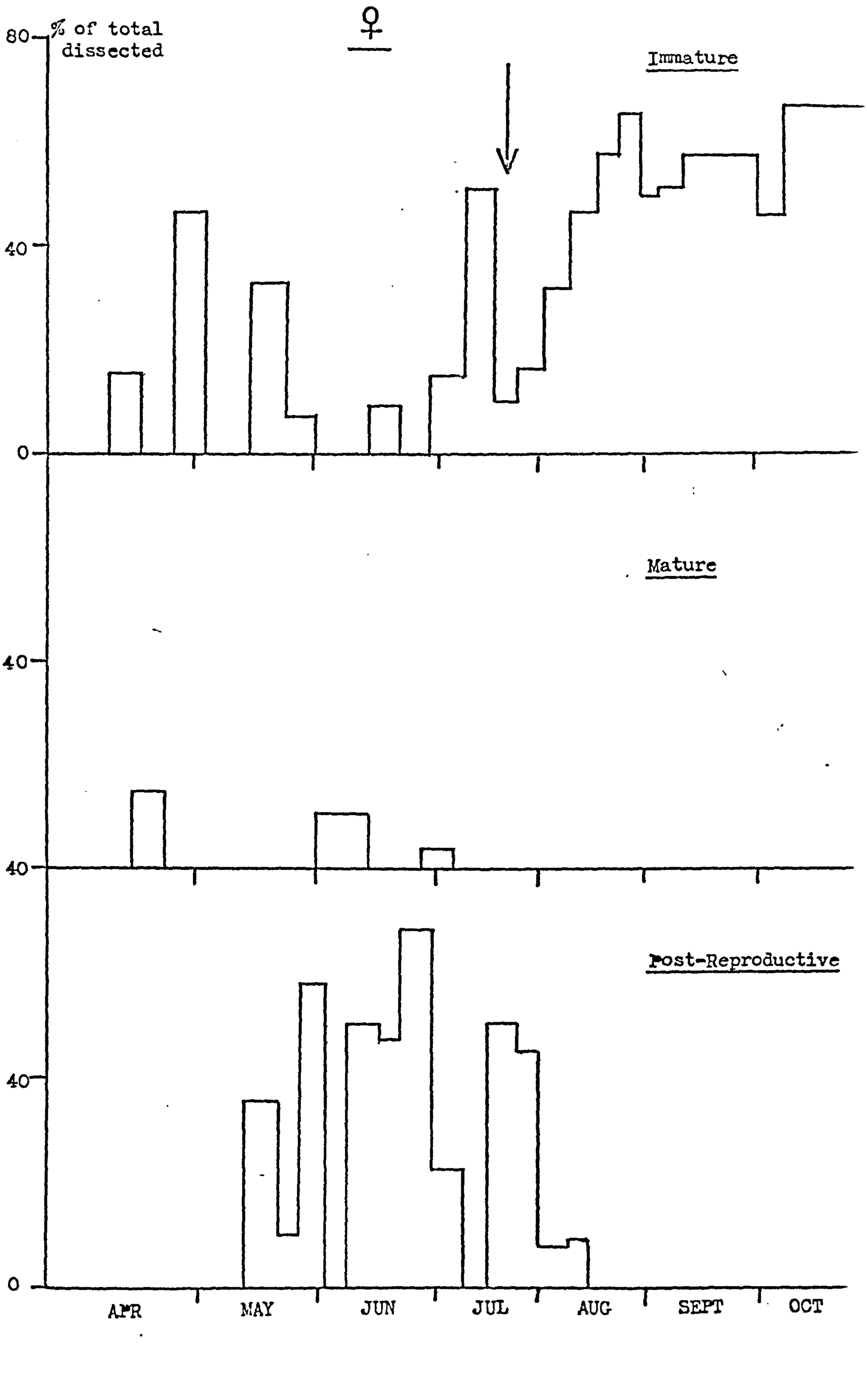
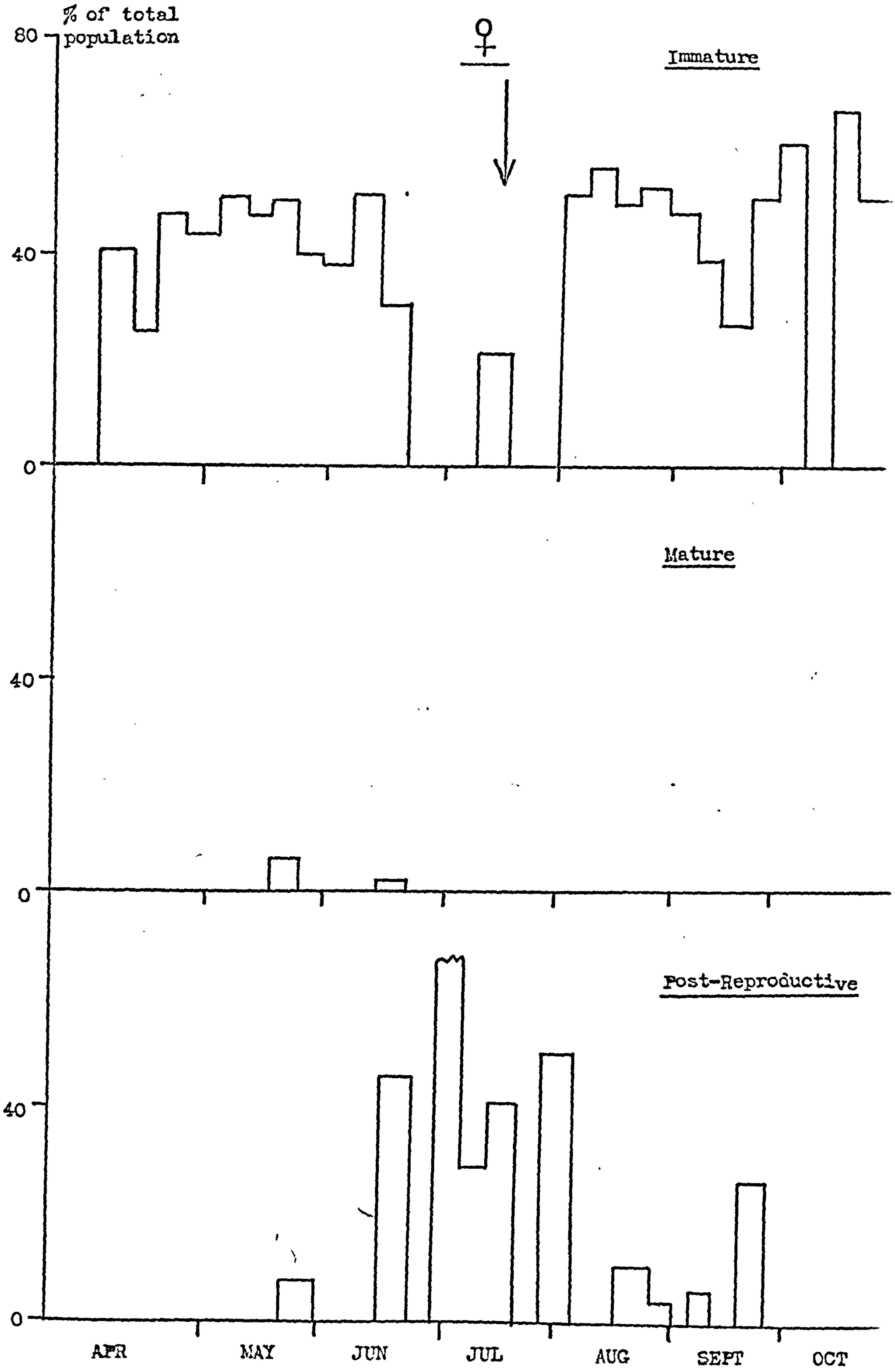

♀
80
% of total dissected
40
0
Immature
Mature
40
Post-Reproductive
40
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

Fig. 2:20

Sexual condition of Necrophorus vespilloides 1974

Symbols as for fig. 2:19.


% of total population
80
40
0
♀
Immature
Mature
40
0
Post-Reproductive
40
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

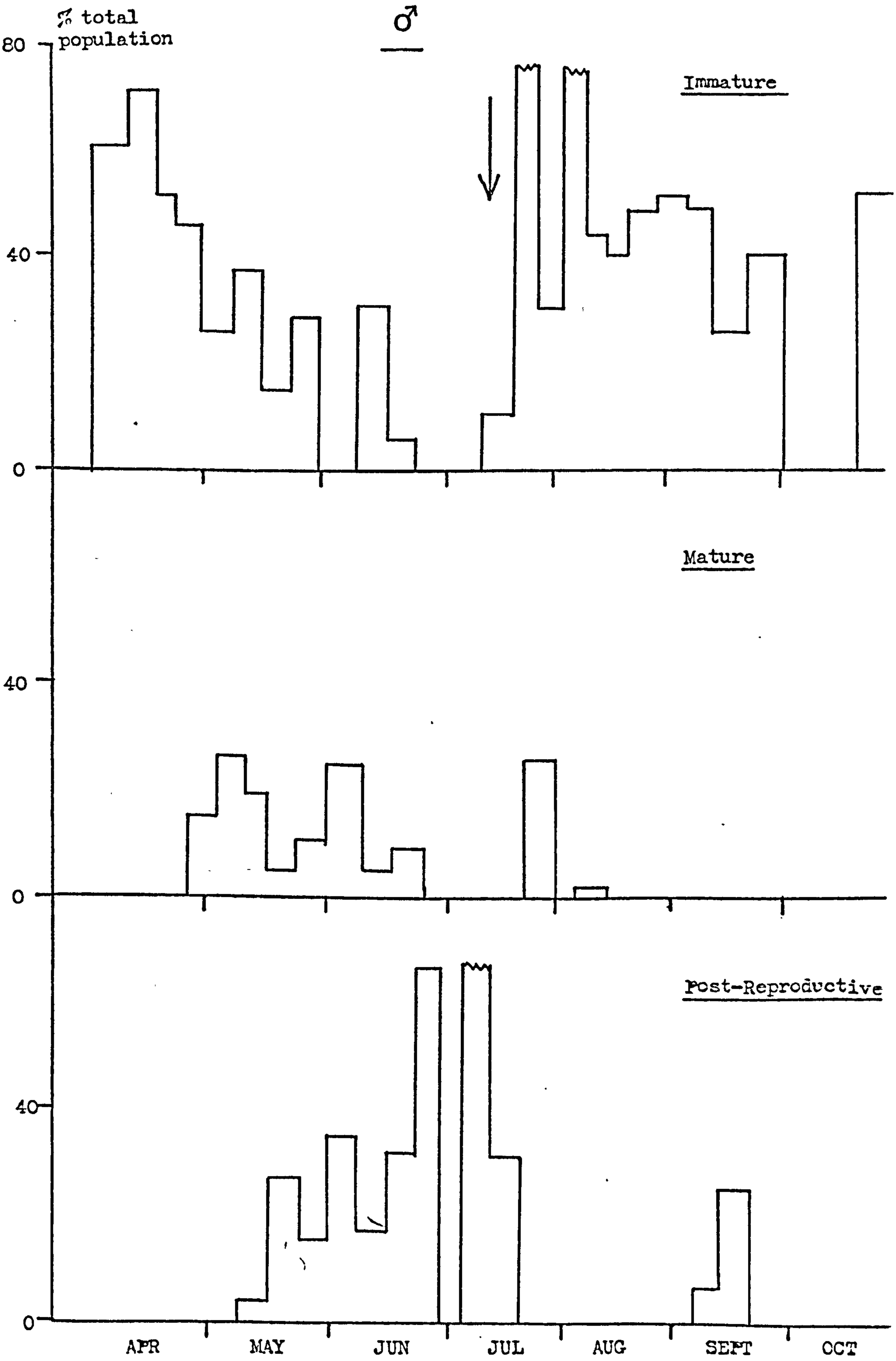
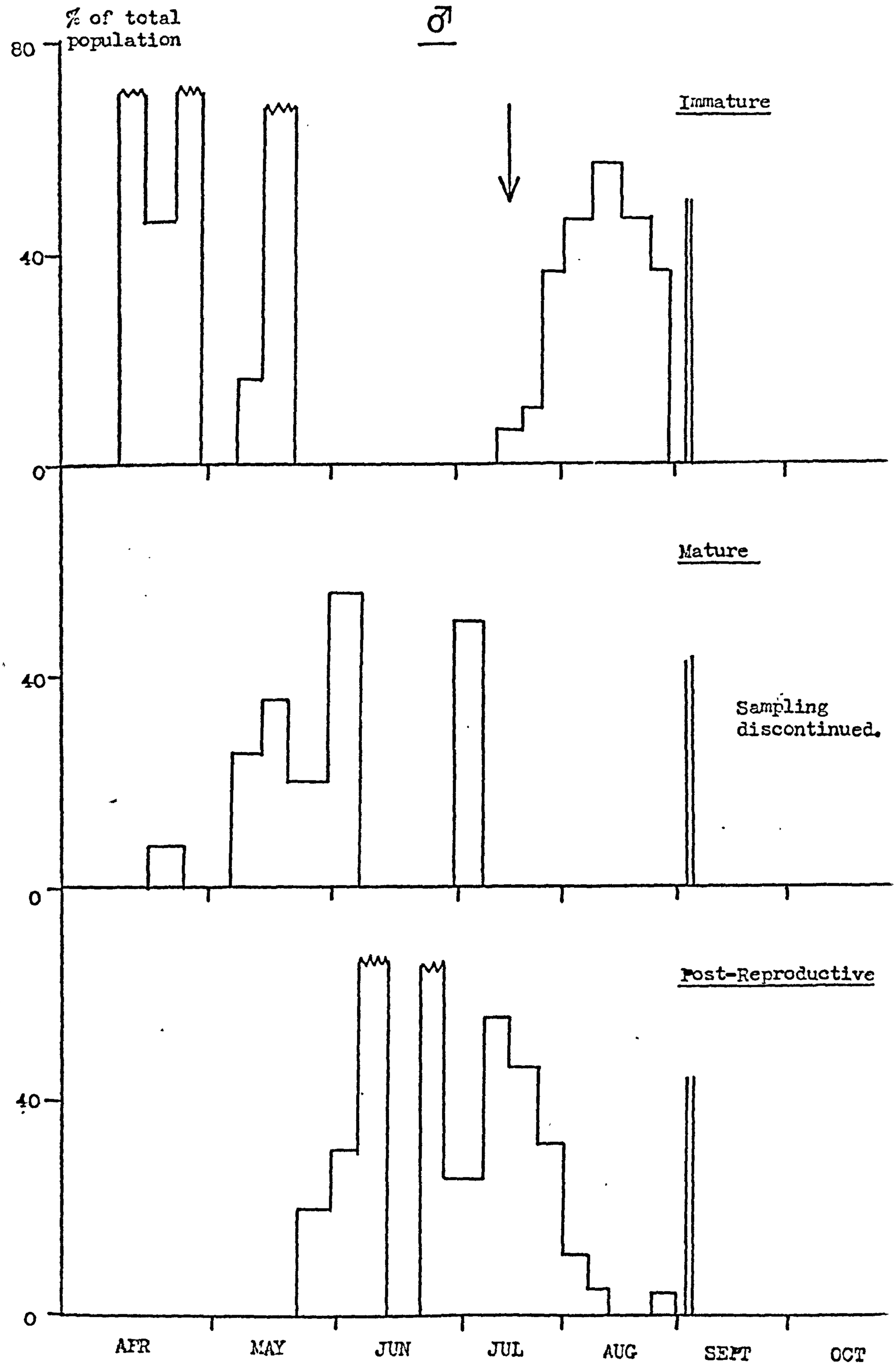

% total population
♂
80
40
0
Immature
Mature
40
0
Post-Reproductive
40
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

Fig. 2:21

Sexual condition of Necrophorus vespilloides 1975

Symbols as for fig. 2:19.


♂
% of total population
80
40
0
Immature
Mature
Sampling discontinued.
Post-Reproductive
40
0
AFR
MAY
JUN
JUL
AUG
SEPT
OCT

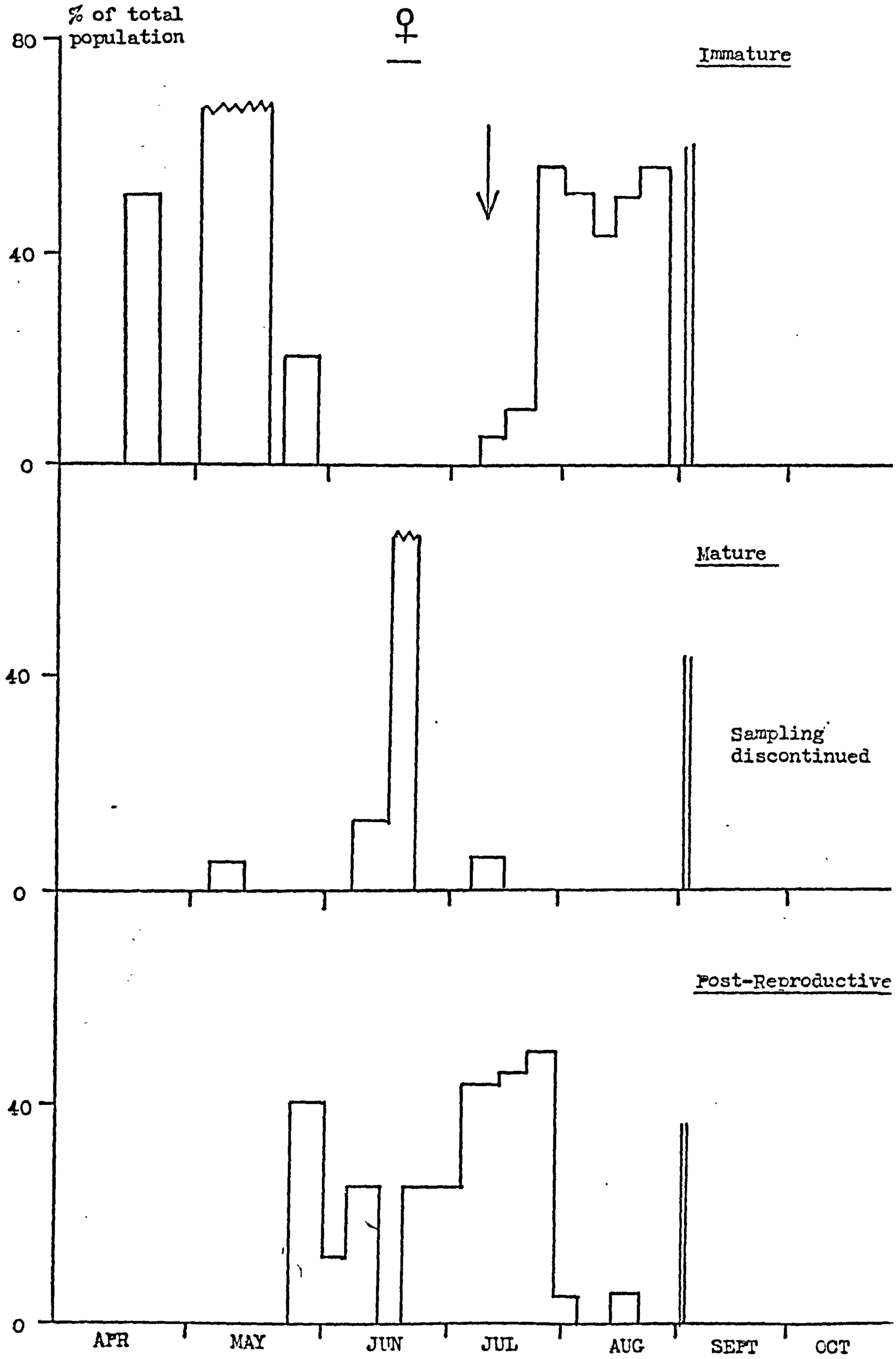

% of total population
80
40
0
♀
Immature
Mature
Sampling discontinued
Post-Reproductive
40
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

Fig. 2:22

Sexual condition of Necrophorus investigator 1973

Symbols as for fig. 2:19

♂

% of total population

Immature

80
40
0

Mature

40
0

Post-Reproductive

40
0

AFR MAY JUN JUL AUG SEPT OCT

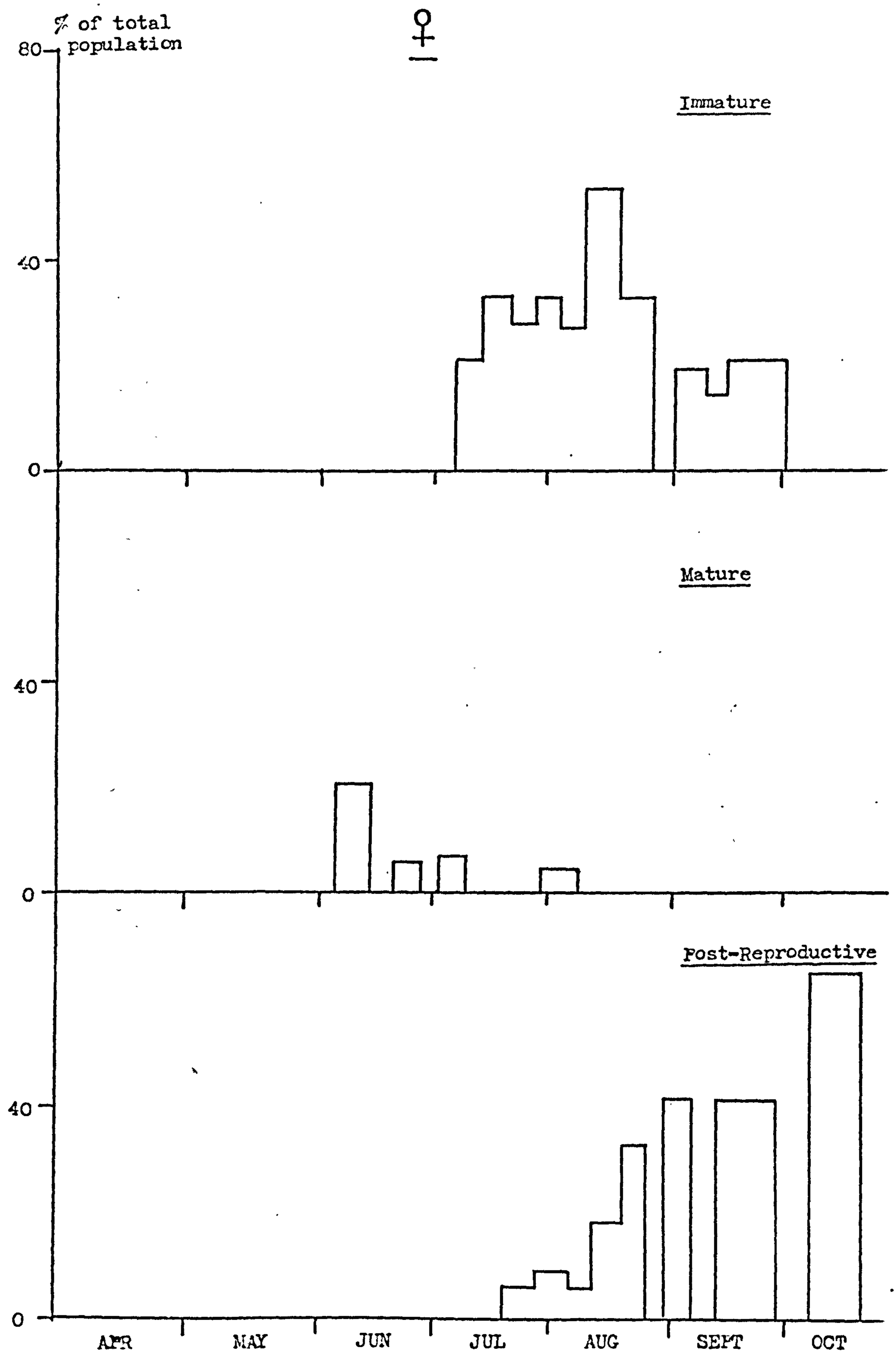

% of total population
♀
Immature
Mature
Post-Reproductive
80
40
0
40
0
0
40
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

Fig. 2:23

Sexual condition of Necrophorus investigator 1974

Symbols as for fig. 2:19

♂

% of total population

Immature

80
40
0

Mature

40
0

Post-Reproductive

40
0

AFR MAY JUN JUL AUG SEPT OCT

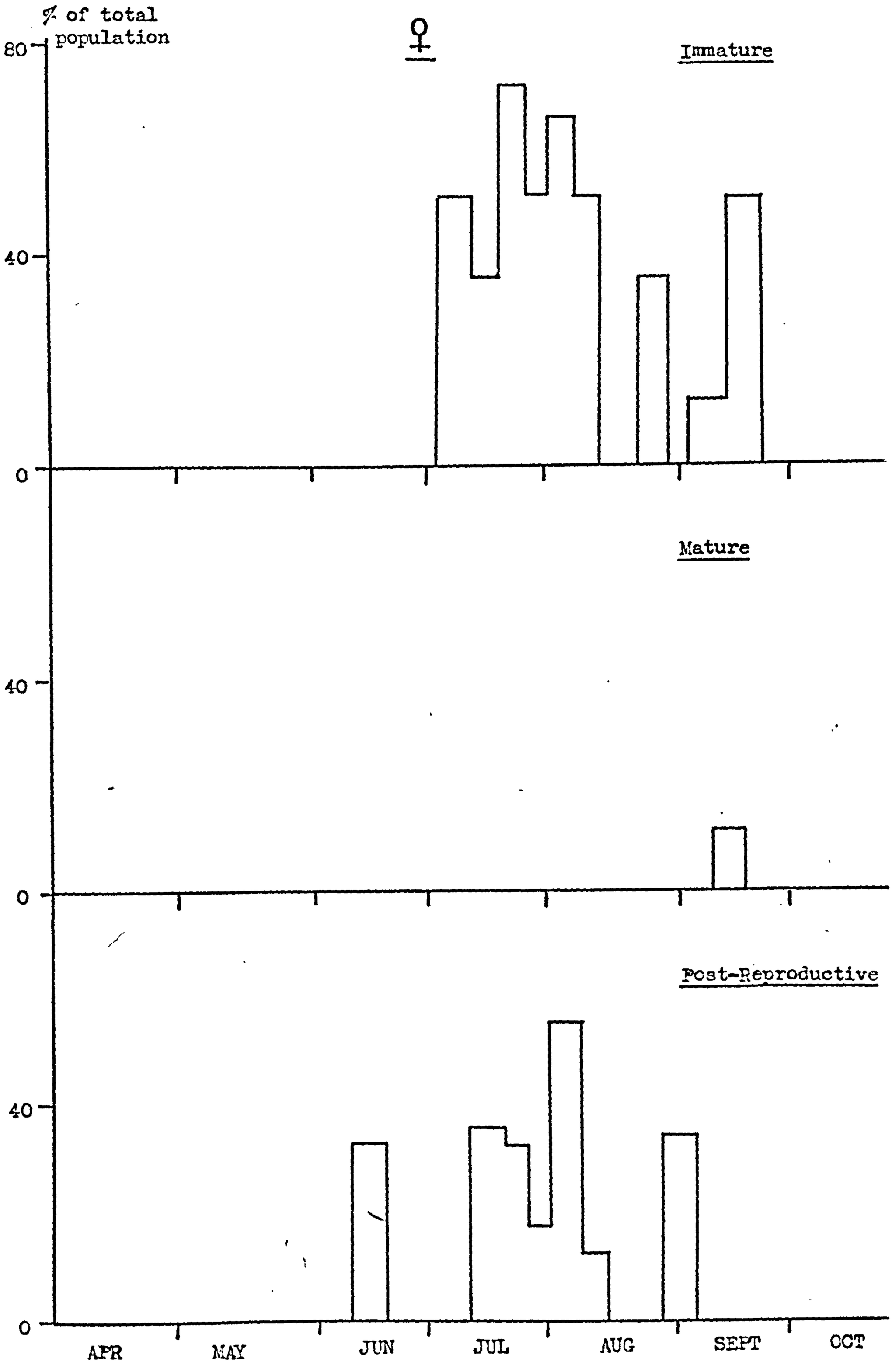
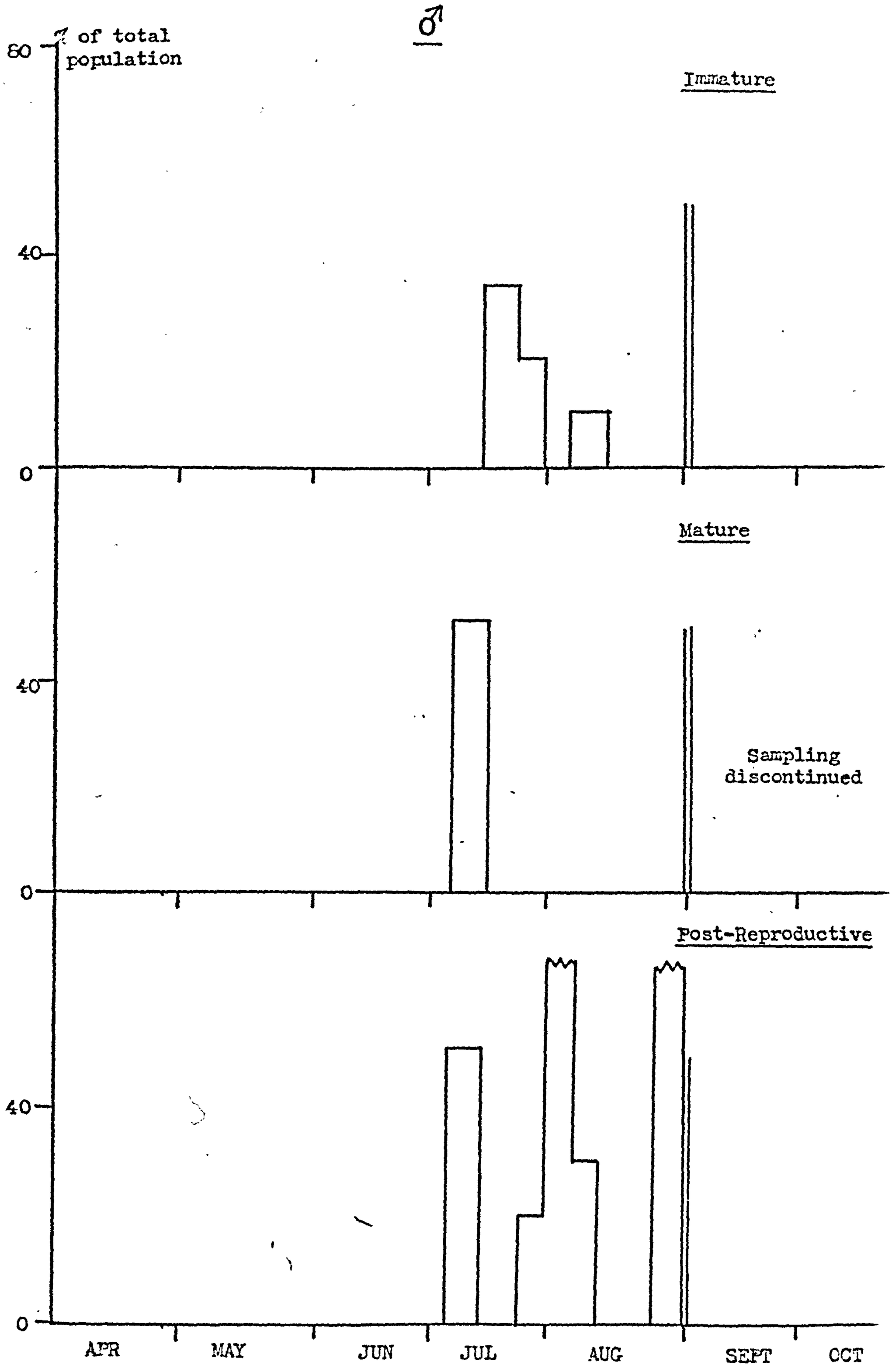
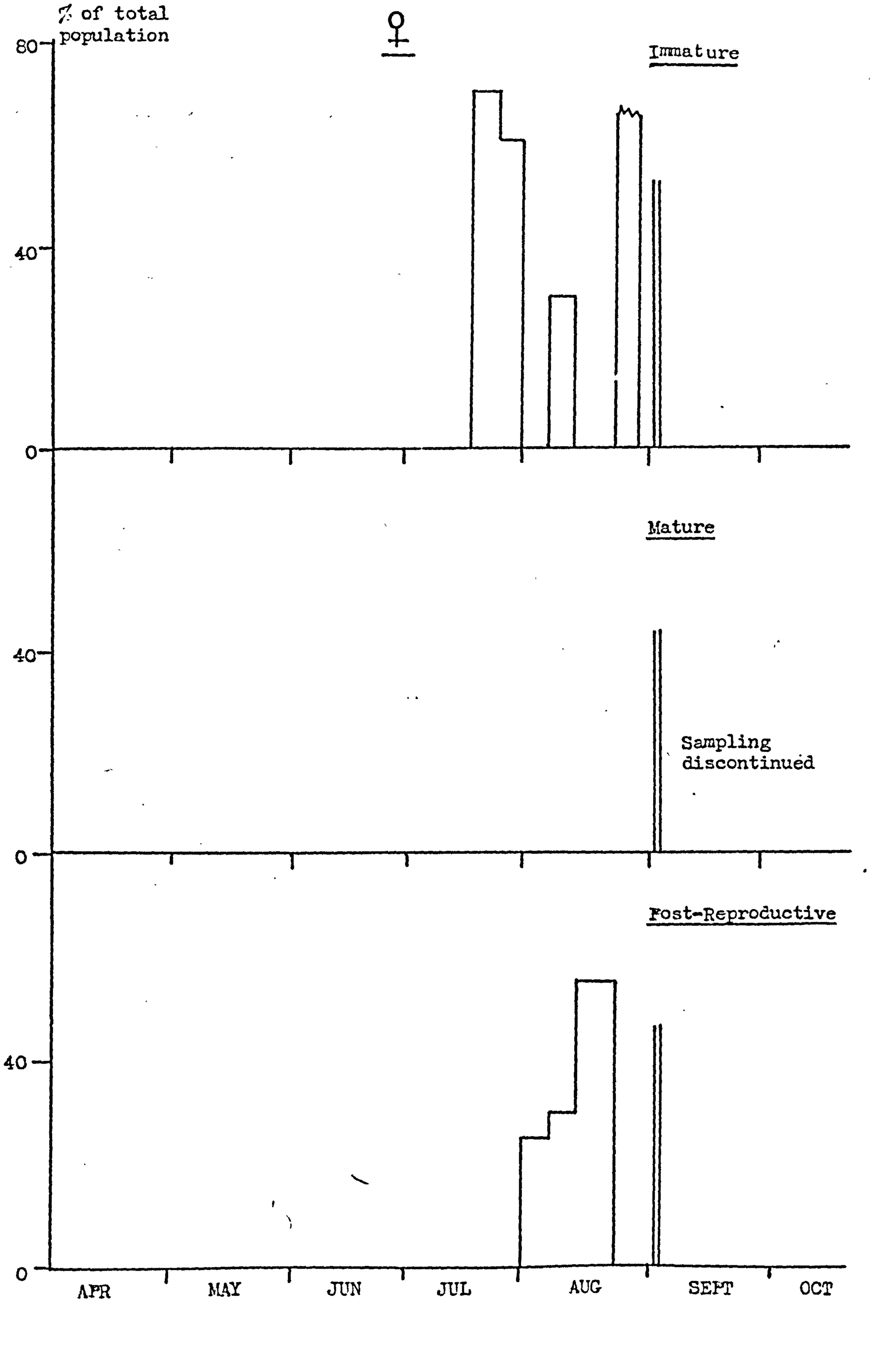

% of total population
80
40
0
♀
Immature
Mature
40
0
Post-Reproductive
40
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

Fig. 2:24

Sexual condition of Necrophorus investigator 1975

Symbols as for fig. 2:19


♂
Immature
% of total population
80
40
0
Mature
40
Sampling discontinued
0
Post-Reproductive
40
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT


% of total population
♀
Immature
80
40
0
Mature
40
Sampling discontinued
0
Post-Reproductive
40
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

1973, the end of August 1974 and the end of July 1975, while post reproductive individuals were found from early May to August 1973, early May to the end of September 1974 and from mid May to August 1975. The delay between the appearance of mature and post reproductive individuals is possibly equivalent to the time taken to breed, i.e. from finding a corpse to emergence of adults from the crypt after the prepupae have dispersed. Just prior to the emergence of immature second generation adults, the N.vespilloides population consists mainly of post reproductive individuals.

Immature and mature N.investigatorappeared at the same time. Some N.investigator, therefore, may have sufficient fat reserves to mature their gonads on emergence from pupation. Immature individuals were present in the population throughout the season. This may indicate that some beetles may not mature their gonads until late in the season, if at all. Mature beetles were present from the beginning of July to mid September 1973, July to October 1974 and from July onwards in 1975. The greatest numbers of post reproductive individuals occurred from August onwards each year. However, some post reproductives were taken early, just as the first immature individuals emerged. These may be individuals which bred the previous year and overwintered. They could not have bred in the year in which they were trapped.

Burial of the corpse, crypt formation, development of larvae and emergence of adults from the crypt after breeding takes about 20 days (Pukowski, 1933). Maximum post reproductive life may be about 10 days (Springett, 1967). An average time of about 30 days may, therefore, elapse from breeding to capture as a post reproductive adult. Using this approximation, and working forward from the last post reproductive recorded each year, crude estimates may be made of the last

dates that N.vespilloides bred. On Inchcailloch these were: end of July in 1973 and 1975 and end of August in 1974. Mature adults were still present after the estimated last date of breeding in 1973, but not in 1974 or 1975. Using the same method of estimation, N.investigator first bred at the beginning of July in 1973, end of July in 1974 and beginning of July in 1975.

2.3.6. Number of Eggs.

The number of eggs in mature females was counted to provide an estimate of the number of eggs actually matured by female burying beetles (Table 2:8). For comparison the number of ovarioles in immature females and number of eggs in post reproductive females was counted. The latter gives an indication of the number of eggs matured but not laid.

The mean number of eggs in mature female N.vespilloides is not significantly different from that in N.humator ($t = 0.722$ doff 14 $p > 0.05$), or N.investigator ($t = 1.04$ doff 14 $p => 0.05$) (Table 2:8). Therefore all three species mature a similar number of eggs. There was no correlation between number of eggs and body length (N.vespilloides $t = 0.10$, d.of.f 8 $p > 0.05$; N.humator $t = 0.411$, d.of.f 4 $p > 0.05$; N.investigator, $t = 0.35$; d.of.f 4 $p > 0.05$) or fat reserves (N.vespilloides $t = 0.27$ d.of.f 8 $p > 0.05$; N.humator $t = 0.311$ d.of.f 4 $p > 0.05$; N.investigator $t = 0.32$ d.of.f 4 $p > 0.05$).

N.humator has the largest eggs, 3.139 ± 0.359mm, and N.vespilloides the smallest, 2.166 ± 0.548mm (Table 2:8). The ratio of egg size to female size is fairly constant, being 1:6.8 for N.vespilloides, 1:7.4 for N.humator and 1:7.9 for N.investigator. Mean egg sizes were not correlated significantly with number of eggs (N.vespilloides

Table 2:8

Number of eggs in female Necrophorus

1. Number of eggs in mature females

	Number of eggs per female			Size of eggs (mm)		
	$\bar{x} \pm$	SD	N	$\bar{x} \pm$	SD	N
N.vespilloides	13.00±	6.566	10	2.166±	0.548	45
N.humator	11.00±	2.323	6	3.139±	0.359	20
N.investigator	9.83±	4.35	6	2.451±	0.434	31

2. Number of eggs in post reproductive females

	Number of eggs per female			Size of eggs(mm)		
	$\bar{x} \pm$	SD	N	$\bar{x} \pm$	SD	N
N.vespilloides	6.545±	4.803	11	2.340±	0.446	33

3. Number of ovarioles

	Number of ovarioles								
	Left ovary			Right ovary			Total		
	$\bar{x} \pm$	SD	N	$\bar{x} \pm$	SD	N	$\bar{x} \pm$	SD	N
N.vespilloides	8.67±3.39		12	7.50±4.12		12	16.67±7.27		12
N.investigator	10.67±2.80		6	12.17±2.86		6	22.83±5.56		6

t = 0.66, d.of f. 8, p>0.05; N.investigator, t = 0.41, d.of f. 4, p>0.05), with female size (N.vespilloides, t = 0.34, d.of f. 8, p>0.05; N.investigator, t = 0.21, d.of f 4, p>0.05), or with fat reserves (N.vespilloides, t = 0.64, d.of f. 8, p>0.05; N.investigator, t = 0.61, d.of f. 4, p>0.05).

On average 6.545 eggs were present in post reproductive N.vespilloides females (Table 2:8). This number is significantly different from that in mature females. Although most of the eggs of a mature female may be laid, some remain in the body after reproduction.

There is no significant difference in number of ovarioles in right and left ovaries (N.vespilloides, t = 0.757, d.of f. 22, p>0.05; N.investigator, t = 0.918, d.of f. 10, p>0.05). The mean number of ovarioles (both ovaries) in female N.vespilloides is 16.67 $\pm$ 7.272, and in female N.investigator, 22.83 $\pm$ 5.655. The difference between the two species was not significant (t = 1.965, d.of f. 16, p>0.05).

As far as could be judged from the small sample available, number of ovarioles was very variable. No significant correlation was found with body length (N.vespilloides, t = 0.210, d.of f. 10, p>0.05; N.investigator, t = 0.510, d.of f. 4, p>0.05) or fat reserves (N.vespilloides, t = 0.190, d.of f. 10, p>0.05; N.investigator, t = 0.76, d. of f. 4, p>0.05).

2.3.7. Fat Reserves.

Fat reserves are well developed in mature individuals and poorly developed in immature individuals (Table 2:9). The weekly variation in the state of the fat body of immature first and second generation, mature and post reproductive N.vespilloides is shown in figs. 2:25 to 2:27. In mature individuals of both sexes it remains well

Table 2:9.

The size of fat body in Necrophorus.

Species and Sexual condition	Size of fat body 1973 ♂ N	$\bar{x} \pm SD$	1973 ♀ N	$\bar{x} \pm SD$	1974 ♂ N	$\bar{x} \pm SD$	1974 ♀ N	$\bar{x} \pm SD$	1975 ♂ N	$\bar{x} \pm SD$	1975 ♀ N	$\bar{x} \pm SD$
N.vespilloides												
Immature (1st gen.)	188	4.90 ± 2.63	191	5.59 ± 2.44	396	5.35 ± 2.31	718	6.53 ± 2.53	129	4.84 ± 1.97	172	5.38 ± 2.28
Mature	117	8.36 ± 1.28	28	9.33 ± 1.15	307	9.58 ± 0.81	30	10.00 ± 0.28	140	9.38 ± 0.98	50	10.21 ± 1.14
Post reproductive	744	6.54 ± 2.37	808	7.28 ± 2.53	640	8.08 ± 1.95	732	7.98 ± 2.17	326	6.32 ± 2.50	374	6.08 ± 2.31
Immature (2nd gen.)	737	3.39 ± 2.62	874	3.09 ± 2.44	607	3.61 ± 2.72	635	3.54 ± 1.71	580	4.17 ± 2.38	534	3.66 ± 2.39
N.humator												
Immature (1st gen.)	2	3.50 ± 2.12	3	6.33 ± 0.58	3	7.67 ± 4.04	8	5.75 ± 3.10	1	6.00 ± 0.00	5	5.20 ± 2.68
Mature	6	8.67 ± 1.63	3	10.00 ± 0.00	4	10.00 ± 0.00	1	10.00 ± 0.00	8	9.38 ± 0.92	1	10.00 ± 0.00
Post reproductive	2	10.00 ± 0.00	5	7.80 ± 2.68	3	10.00 ± 0.00	3	9.67 ± 0.58	1	10.00 ± 0.00	1	6.00 ± 0.00
Immature (2nd gen.)	42	4.40 ± 2.51	44	4.68 ± 3.24	8	5.75 ± 2.51	8	8.63 ± 2.45	3	0.00 ± 0.00	2	2.50 ± 0.71
N.investigator												
Immature	39	4.44 ± 3.08	36	5.42 ± 3.29	11	3.9 ± 2.43	15	7.00 ± 3.23	3	5.33 ± 1.15	11	5.36 ± 2.62
Mature	14	8.50 ± 1.91	5	9.80 ± 0.45	4	10.00 ± 0.00	2	10.00 ± 0.00	1	10.00 ± 0.00	No data	
Post reproductive	21	7.52 ± 2.09	26	8.73 ± 1.54	13	8.31 ± 2.53	5	9.20 ± 1.09	9	7.56 ± 2.35	7	9.14 ± 1.21

Fig. 2:25

Variation in size of fat body : N.vespilloides 1973

——— = Immature

- - - - = Mature

—·—· = Post reproductive

* = first emergence of second generation immature

↑ = small number of individuals

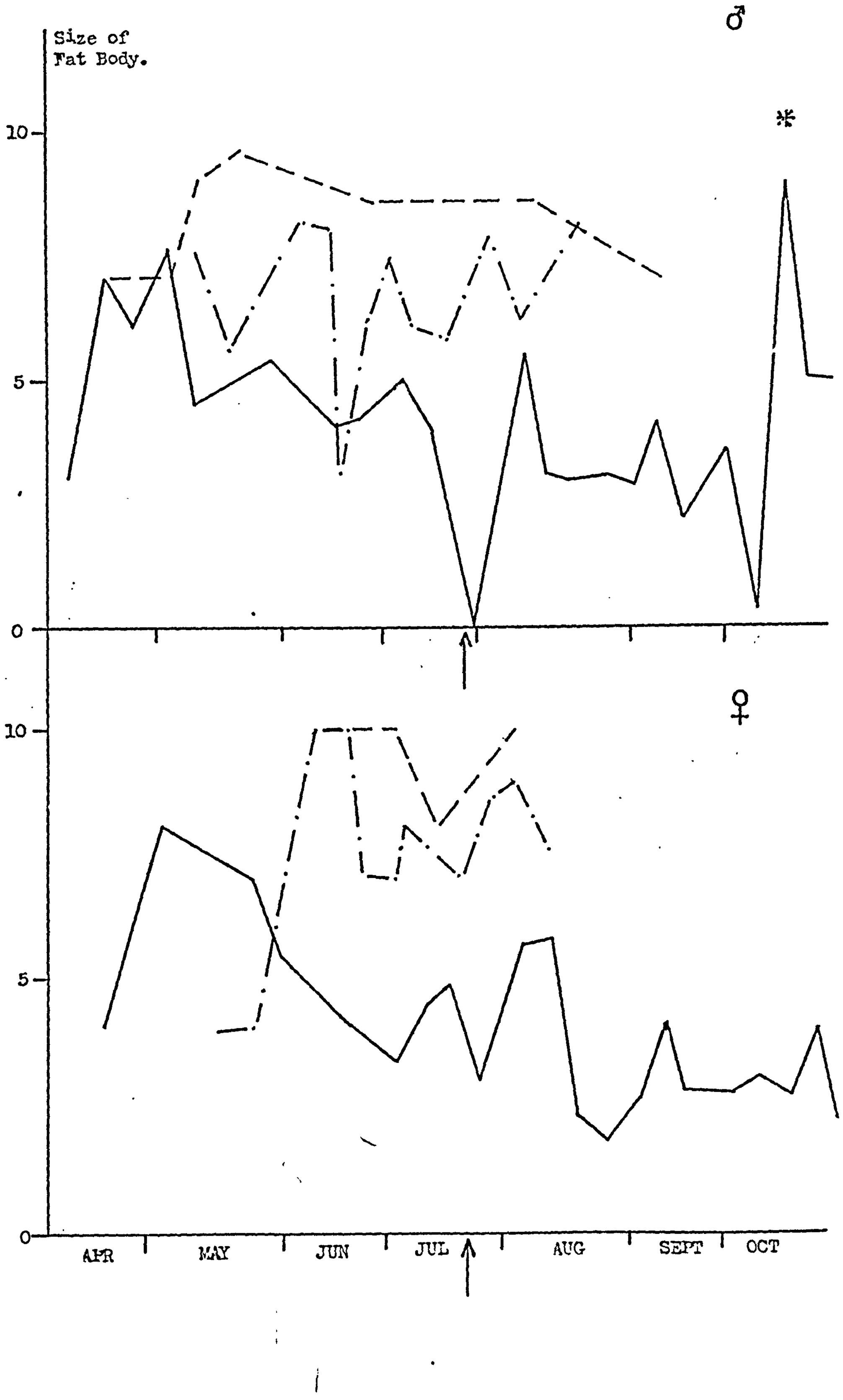

♂
Size of
Fat Body.
10
5
0
♀
10
5
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

Fig. 2:26

Variation size of fat body : N.vespilloides 1974

Symbols as for fig. 2:25

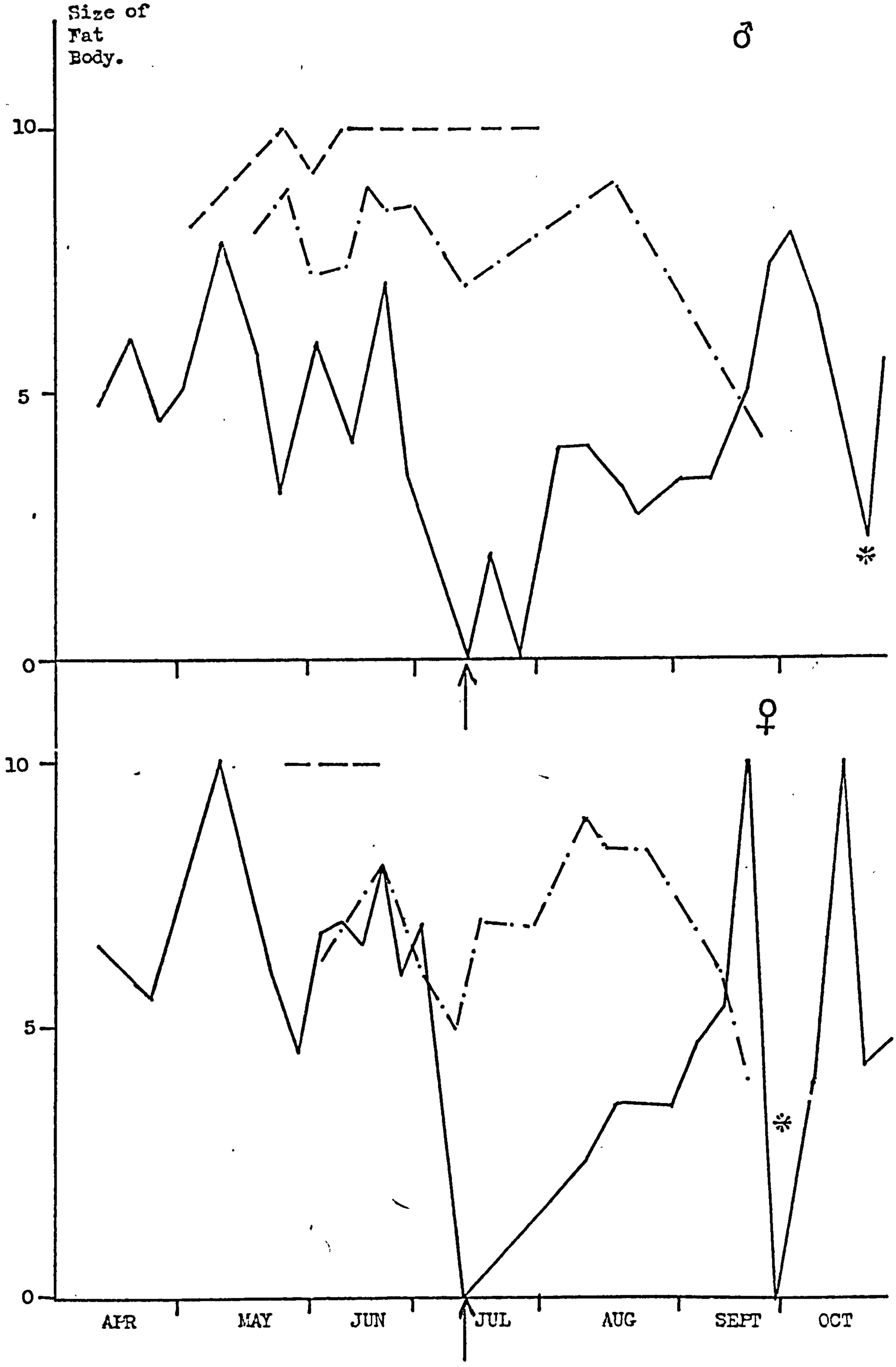
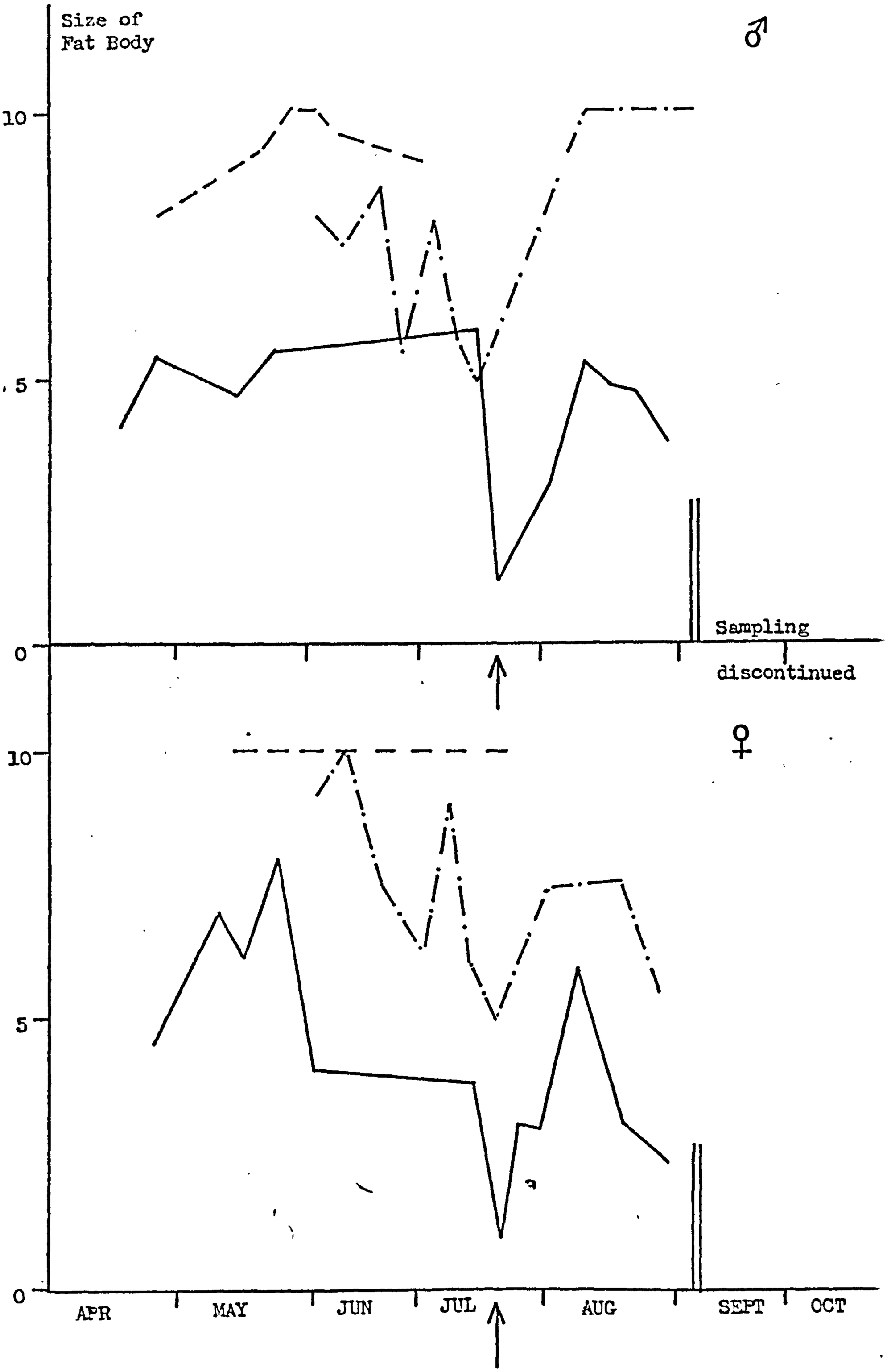

Size of
Fat
Body.
10
5
0
♂
♀
10
5
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

Fig. 2:27

Variation in size of fat body : N.vespilloides 1975

Symbols as for fig. 2:25


Size of
Fat Body
10
.5
0
♂
Sampling
discontinued
♀
10
5
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

developed throughout the year, but takes about a month to develop at the beginning of the year. In post reproductive individuals, the fat body is in an intermediate state of development. In 1974, post reproductive adults were found later in the season than in 1973. A rapid decline in fat reserves in both sexes occurred during August and September and may indicate a shortage of food for post reproductive adults emerging from the crypt.

Over the period of the study, immature individuals of N.vespilloides showed variation in the state of development of the fat body. Immature individuals had, on average, smaller fat bodies when the callow adults of the second generation entered the population. These beetles have very small fat reserves after emergence from the pupa. The fat body of immature second generation adults varied differently each year. In 1973, a steady decline in the size of the fat body was observed from July to October, while in 1974, the fat body of immature adults increased in size over the same period. In 1975, the mean fat body size decreased at the end of August. This would suggest that in 1973 and 1975 there was insufficient food for individuals of the second generation of N.vespilloides to accumulate fat. In 1974 there was sufficient food for beetles to accumulate fat, and as a result, their fat reserves increased in size up to the end of the season.

Too few N.humator were trapped to draw any conclusions (Table 2:9), but in general, weekly variation seemed similar to that of N.vespilloides. The fat reserves of mature N.investigator were constantly high (fig. 2:28 to 2:20)., while those of immature and post reproductive individuals varied. No trends in the fat reserves of N.investigator were observed.

Fig. 2:28

Variation in size of fat body : N.investigator 1973

Symbols as for fig. 2:25

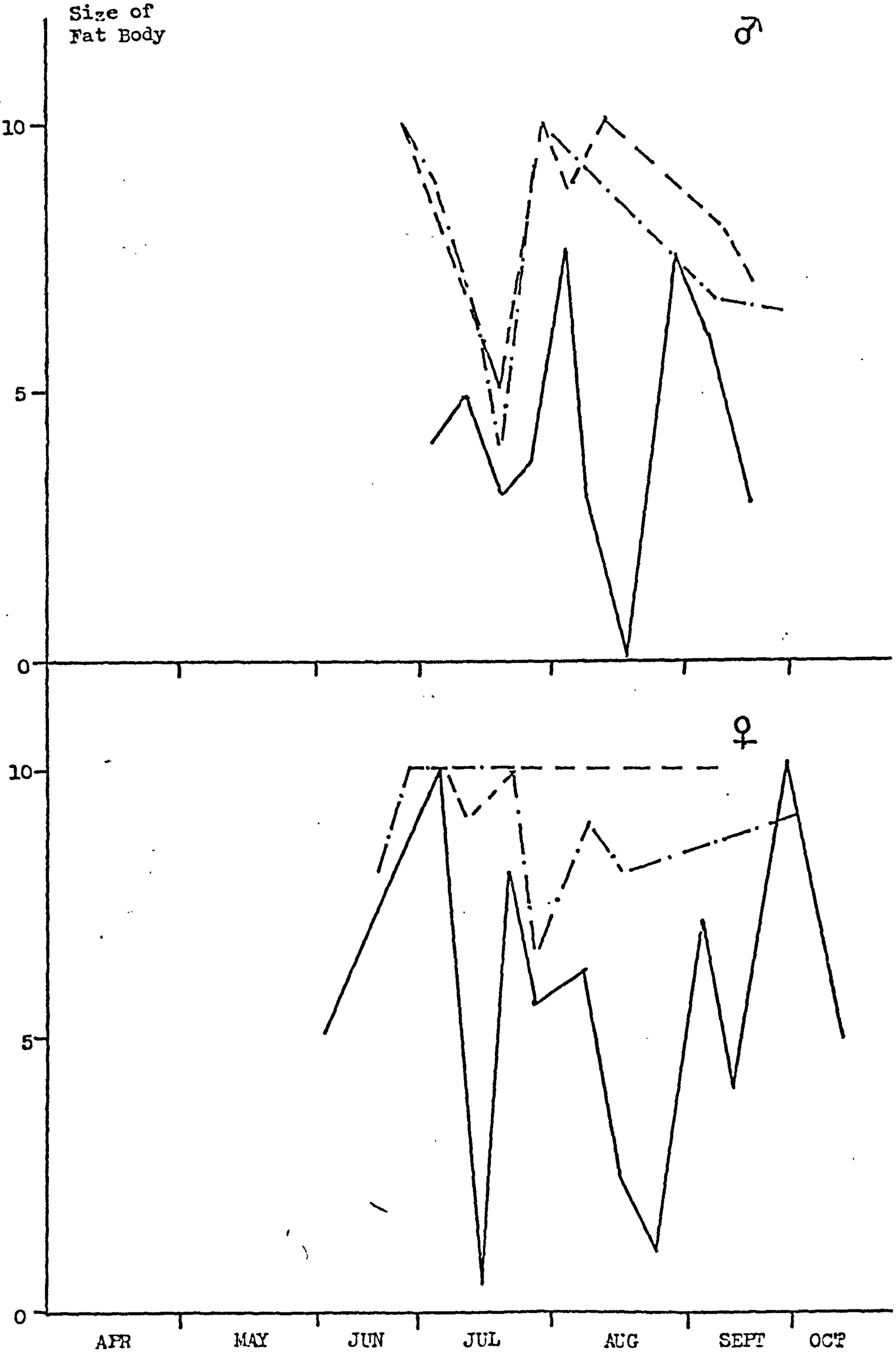

Size of
Fat Body
♂
10
5
0
♀
10
5
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

Fig. 2:29

Variation in size of fat body : N.investigator 1974

Symbols as for fig. 2:25

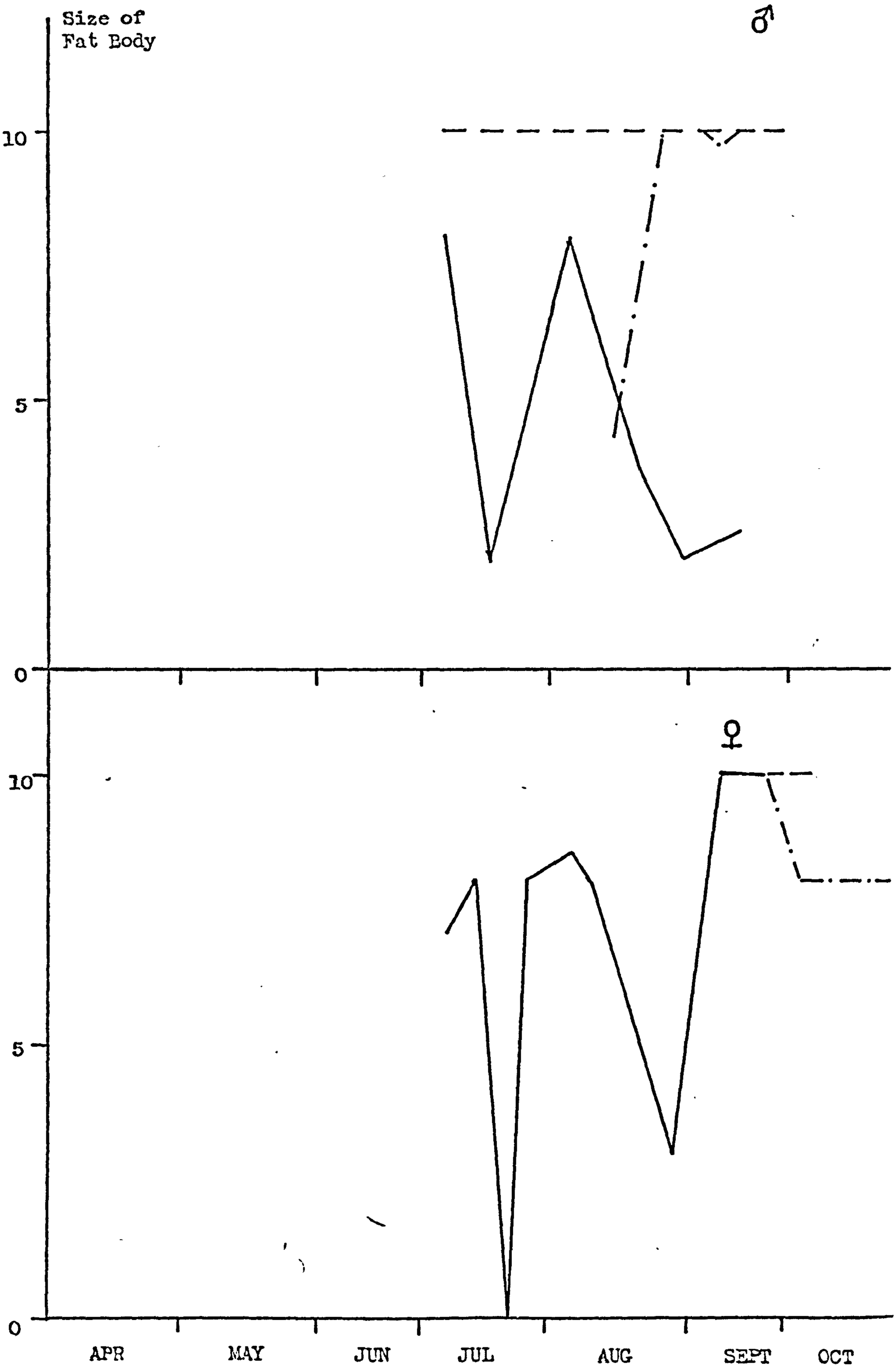
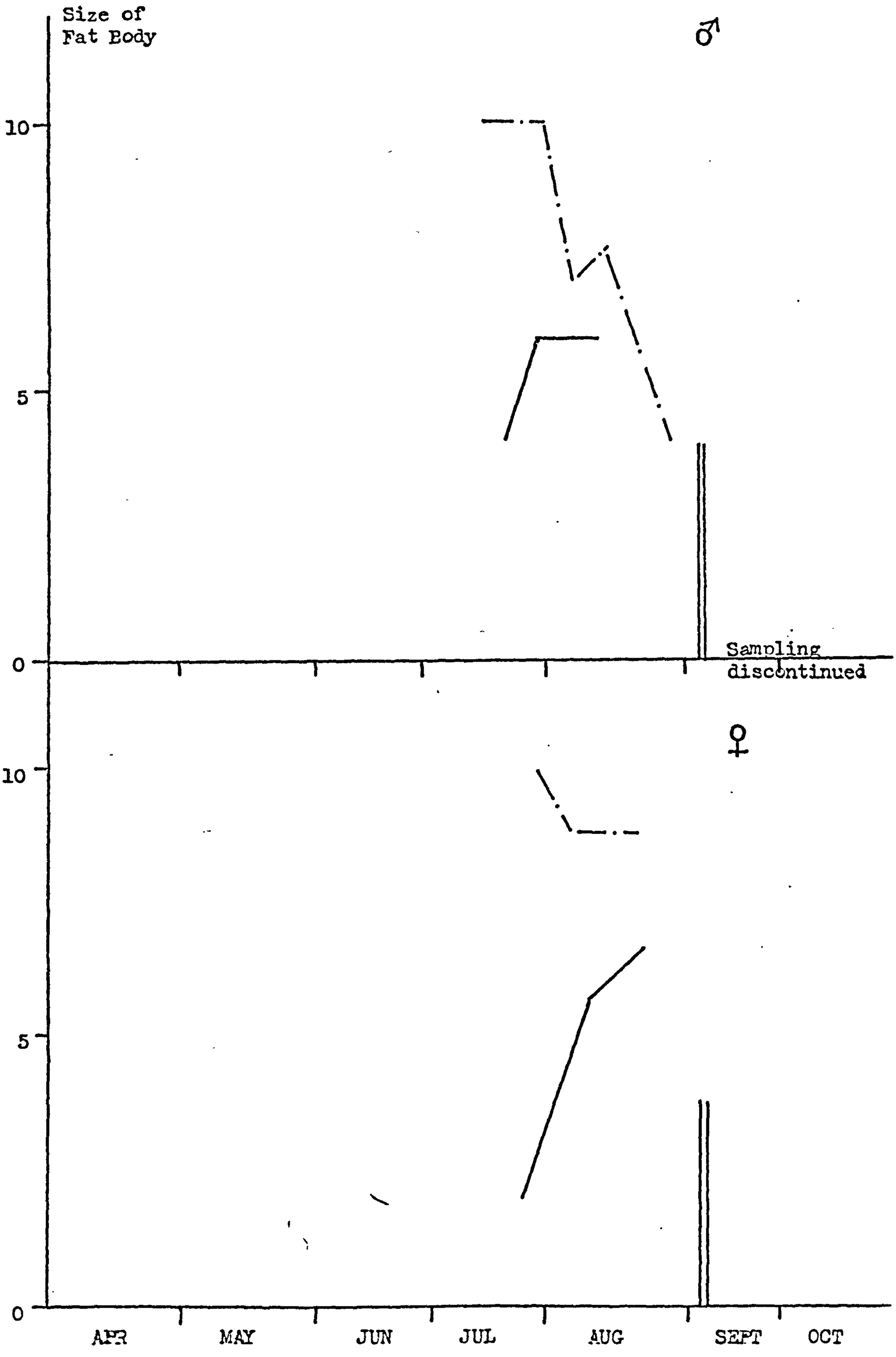

Size of
Fat Body
♂
10
5
0
♀
10
5
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

Fig. 2:30

Variation in size of fat body : N.investigator 1975

Symbols as for fig. 2:25


Size of
Fat Body
10
5
0
♂
Sampling
discontinued
♀
10
5
0
APR
MAY
JUN
JUL
AUG
SEPT
OCT

There is a significant, although weak, relationship between the size of immature N.vespilloides and N.humator individuals, and the size of their fat body (fig. 2:31). Mature and post reproductive individuals of these species do not show such a relationship. There is, however, a significant correlation between body length and size of fat body for mature and post reproductive N.investigator (fig. 2:31). These results are difficult to explain. Large beetles may be able to acquire more food than smaller individuals, but no explanation can be offered for the differences between species.

The subjective estimate of fat reserves is correlated with the amount of fat actually present, measured by extraction (fig. 2:32). The amount of fat present in the body was expressed as: a) % of dry weight of the abdomen, b) % of wet weight of the abdomen and c) % of original body weight. The best relationship between the qualitative and quantitative estimates is when fat reserves are expressed as a percentage of the dry weight of the abdomen. This indicates the amount of fat present in the abdomen, which is also the basis of the subjective estimate. The closeness of the relationship suggests that the qualitative assessment is a good estimate of the amount of fat in the abdomen and so its use during the population study was justified. The qualitative estimate is less closely correlated with fat expressed as a percentage of abdominal weight, or as a percentage of body weight (fig. 2:32). This is to be expected, as other factors, such as the amount of water present, will vary in these estimates.

2.3.3. Mark-Recapture Studies.

The only previous attempt to analyse a population of burying beetles using mark-recapture techniques was made by Springett (1967), on Inner Farne Island. In that study, the population estimates were

Fig. 2:31

Relationships between body size and fat reserves.
Each dot is the mean of all fat bodies for this size class. The bar represents standard deviation.
Correlations were performed on all data.

N.vespilloides (immature)

Fat Body

♂ y = 2.64x + 1.69
♀ y = 3.11x + 1.88

♂ r = 0.221 d.of f, 657 p<0.05
♀ r = 0.226 d.of f. 746 p<0.05

N.humator (immature)

both sexes, y = 2.78x + 1.963

r = 0.226 d.of f. 56 p<0.01

N.investigator (mature)

both sexes, y = 2.95x + 3.221

r = 0.479 d.of f. 18 p<0.05

N.investigator (post-reproductive)

♂ y = 2.72x + 2.381
♀ y = 2.87x + 3.308

♂ r = 0.321 d.of f. 41 p<0.05
♀ r = 0.486 d.of f. 37 p<0.05

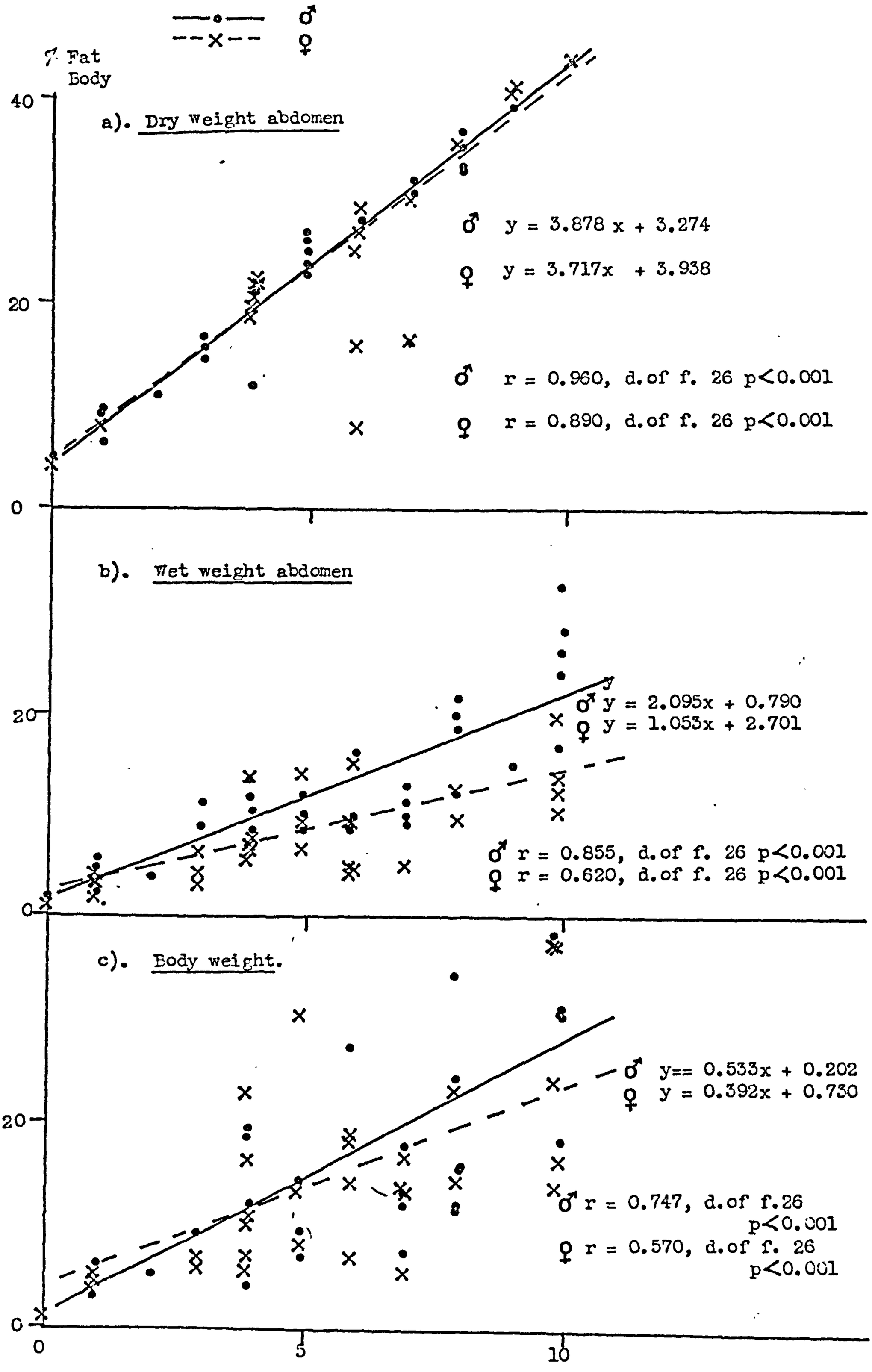
0 5 10

1.5 2.0 1.5 2.0

Body length (cm.)

Fig. 2:32

Relationship between the qualitative estimate of fat reserves and the amount of fat obtained by extraction.


♂
♀
% Fat Body
40
20
0
a). Dry weight abdomen
♂ y = 3.878 x + 3.274
♀ y = 3.717x + 3.938
♂ r = 0.960, d.of f. 26 p<0.001
♀ r = 0.890, d.of f. 26 p<0.001
b). Wet weight abdomen
♂ y = 2.095x + 0.790
♀ y = 1.053x + 2.701
♂ r = 0.855, d.of f. 26 p<0.001
♀ r = 0.620, d.of f. 26 p<0.001
c). Body weight.
♂ y== 0.533x + 0.202
♀ y = 0.392x + 0.730
♂ r = 0.747, d.of f.26 p<0.001
♀ r = 0.570, d.of f. 26 p<0.001
0
5
10
Qualitative assessment of fat body.

regarded only as a rough guide to the numbers present, due to the low incidence of recapture. A more detailed analysis was not anticipated during this study, for several reasons. The habitat on Inchcailloch is considerably more complex than on treeless Inner Farne island. The short distance to the mainland means that Inchcailloch is considerably less isolated than Inner Farne, there is no guarantee that the population on Inchcailloch is an isolated one, or will be amenable to the mark-recapture techniques used. Finally, the incidence of recapture was even lower than that obtained by Springett (1967), and as a result, analysis of N.vespilloides captures only could be attempted. Analysis was expected only to provide a rough estimate of the numbers present.

2.3.8.1. Estimate of Immigration and Emigration.

Emigration was estimated by calculating the proportion of beetles marked on Inchcailloch or the mainland and recaptured in a different area. Immigration was estimated by finding the proportion of beetles captured on Inchcailloch or the mainland which had been marked elsewhere.

Emigration from Inchcailloch was less than 5% and varied little from year to year (Table 2:10). Immigration varied between 0% and 11%. In the first two years there was more immigration than emigration on Inchcailloch, with a net immigration rate of 0.85% in 1973, and 7.88% in 1974. In 1975 there was a net emigration of 1.92%. A much higher proportion of beetles seemed to move on and off the mainland, but the number of recaptures of mainland individuals was too small to investigate this difference.

Emigration and immigration may occur mainly among first generation (breeding) adults. 89% of the individuals recorded as

Table 2:10

Movement of marked beetles between sampling areas.

	Emigration		Immigration	
	Inchcailloch	Mainland	Inchcailloch	Mainland
Year	(% marked Inch. recaptured elsewhere)	(% marked Main. recaptured elsewhere)	(% marked elsewhere recaptured Inch.)	(% marked elsewhere recaptured Main.)
1973	3.57	75.00	4.42	75.00
1974	2.94	66.67	10.82	50.00
1975	1.92	0.00	0.00	33.33

Note Emigration and immigration are calculated as percentages of the total number of beetles recaptured in each area.

immigrants or emigrants during 1973, and 80% in 1974 were first generation adults. These individuals are known to fly long distances in search of a corpse for breeding (Petrůska, 1964; Springett, 1967).

2.3.8.2. Estimate of Population size.

The mark-recapture data was analysed using the method described by Jolly (1965) and summarised by Southwood (1966). This was one of the methods used by Springett (1967) to estimate burying beetle population numbers on Inner Farne. This method allows for changes in population due to death, emigration and immigration and for any losses that may occur between capture and release - "losses on capture".

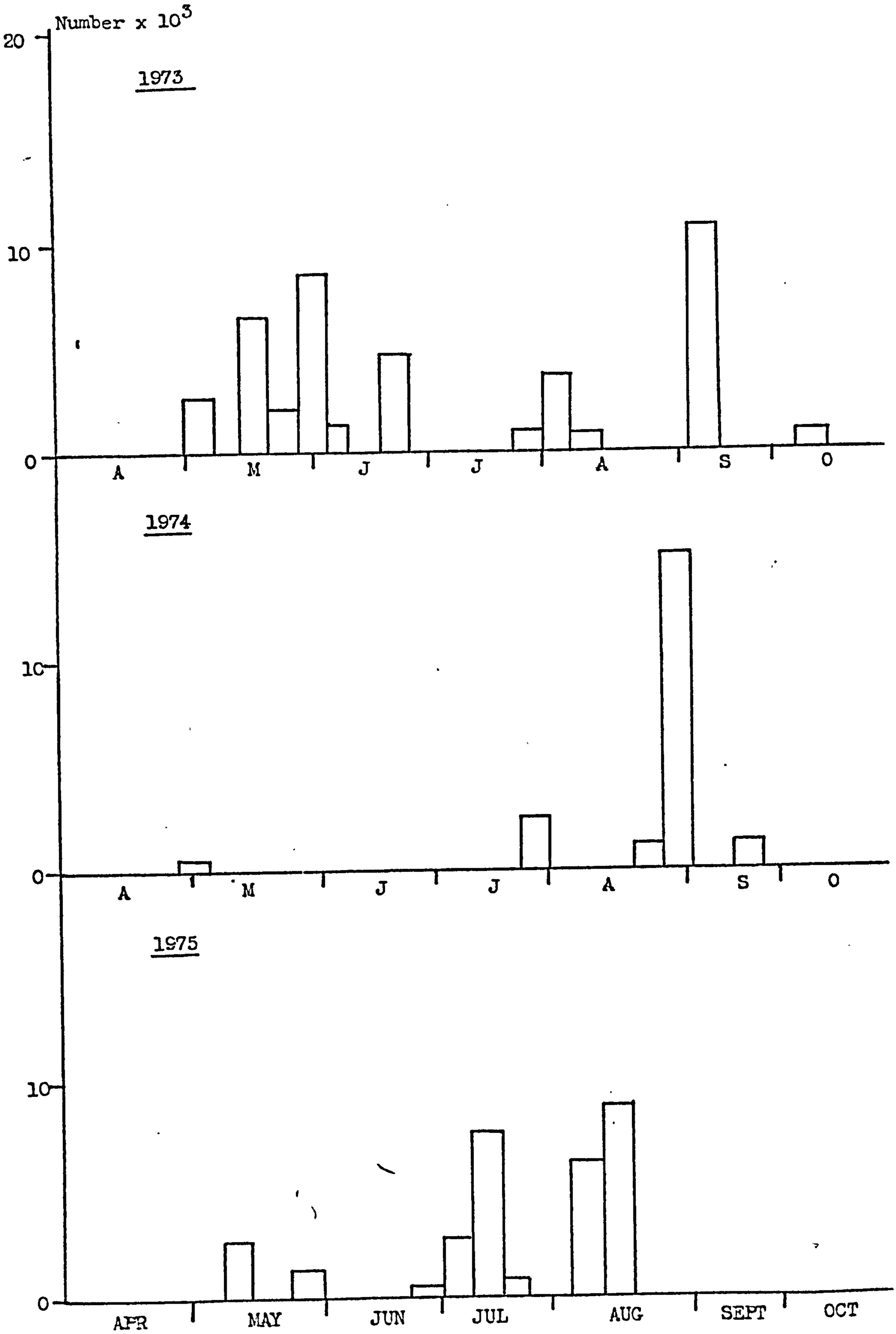
Southwood (1966) lists a number of assumptions which must be tested before Jolly's method is used, namely:

a) Marked individuals are not affected by being marked and marks will not be lost.
b) Marked beetles become completely mixed in the population.
c) All individuals of different age groups and of both sexes are sampled in the proportions in which they occur.
d) All individuals are equally available for capture irrespective of their position in the habitat.
e) Being recaptured does not affect an animal's subsequent chances of capture.

These assumptions were tested as far as possible, and found to hold, and so Jolly's method was considered satisfactory. The detailed steps and results are set out in Appendix 3. Only in 1973 were there sufficient recaptures to give a reasonable estimate of population numbers (fig. 2:33). In 1974 and 1975, no reliable estimates were possible. Even in 1973, the estimates are crude and more detailed analysis was not carried out.

Fig. 2:33

Population estimates for N.vespilloides


Number x 10^3
20
10
0
1973
A
M
J
J
A
S
O
1974
10
0
A
M
J
J
A
S
O
1975
10
0
AFR
MAY
JUN
JUL
AUG
SEPT
OCT

In general, the population estimates for 1973 show a similar distribution to that of the trapping records (fig. 2:10). Peaks occur at the same time, and the second peak of immature second generation adults is higher than the first peak. This suggests that the trapping records may give a good estimate of changes in abundance of beetles throughout the year.

The number of beetles trapped is a very small proportion of the estimated total population. For example, 145 beetles were trapped in late May 1973, from an estimated population of 8000 (i.e. 1.8%), and 370 from an estimated population of 10,366 in late August 1973 (i.e. 3.57%). With such a large population, dispersed over a large area (54 ha), it is not surprising that few marked individuals were recaptured. Any future mark-recapture study would have to trap and mark many more beetles, by increasing trap density.

On Inner Farne island, which is about 7 ha in size, Springett (1967) trapped and marked nearly 50% of the estimated population of N.investigator (about 400 individuals). This gives a density of about 55 N.investigator per hectare on Inner Farne, compared with about 148 N.vespilloides per hectare on Inchcailloch in May 1973. Although a slightly smaller insect, N.vespilloides appears to have a very much higher density in Inchcailloch than does N.investigator on Inner Farne island. Such a large population of burying beetles could perhaps be expected in the complex habitat provided by an oakwood.

2.3.9. Availability of Carrion in the Study Area.

One of the major resources needed by an adult burying beetle is a corpse for breeding. Without suitable carrion at the correct time of year, Necrophorus cannot breed. To complement the field study of the

Necrophorus population, the type and occurrence of carrion likely to be available to burying beetles in the study area was examined.

Although it is a National Nature Reserve, there is little quantitative information available on the vertebrate populations of Inchcailloch. Indeed, this type of information is available for few areas in Britain. It is impossible, therefore, to estimate the quantity of carrion available to the burying beetles on Inchcailloch. However, by synthesising data from various sources it is possible to estimate the type of carrion available, when it will occur and the relative proportions of each type. This information is summarised in Table 2:11, and the steps by which these estimates were synthesised are set out in Appendix 3.

From April to July, the carrion potentially available to burying beetles will consist mainly of the corpses of juvenile shrews (c. 7 gms), adult shrews (c. 10 gms), adult and juvenile bank voles and field voles (10-30 gms) and nestling birds of various species. From July to September, the corpses of juvenile and adult shrews will occur, together with those of fledgling birds, most weighing less than 20 gms.

The variety of carrion available to N.vespilloides is greater than that available to N.investigator. Further, as birds may be less abundant on Inchcailloch than small mammals, particularly bank voles, the relative number of corpses available to N.investigator may be less than that available to N.vespilloides. In the absence of more information, a more detailed statement cannot be made.

Deer carcasses may be suitable for the breeding of N.humator, which are thought to breed on large corpses (Portevin, 1926a). About 3 adults and 6 fawn corpses may be found in Inchcailloch each year, all from April to July, the breeding season of N.humator.

Table 2:11

The availability of carrion on Inchcailloch

(See Appendix 3).

Type of Corpse	(Numbers)	Size	When available
Shrew	Adults	c 10gms	April - July August - October
	Juveniles (numbers unknown)	c 7gms	May - October
Bank vole	Adults	c 30gms	April - July (peak June) (Death rate lowest July - September)
	Juveniles (numbers unknown)	10 - 30gms	
Field vole	Adults	c 30gms	April - June (peak May) (Death rate lowest July - September)
	Juveniles (number unknown)	10 - 30gms	
Birds	Adults	9 - 1000gms	Unknown
	Nestlings	< 60gms	Most before June, some throughout summer
	fledglings	< 100gms (most < 20gms)	June - November
Fallow deer	adults (2)	63 - 110kg	April/May
	fawn (1)	4 - 5kg	
Roe deer	Adults (2-3)	c 110kg	April - September
	Kids (6)	1 - 8kg	May/June

2.4. Discussion

The different life cycles of N.investigator and N.vespilloides result in different patterns of abundance during the year. The offspring of N.investigator remain underground as prepupae emerging the following summer. As a result, only one peak in numbers is observed each year, consisting of immature, breeding and post reproductive individuals. The offspring of N.vespilloides overwinter as immature adults, which emerge to feed before going into diapause. The population of N.vespilloides has two peaks, the first consisting of immature, breeding and post reproductive individuals, the second of immature second generation adults. Variations in the size of the second peak occur from year to year and these may reflect changes in the breeding success of the first generation. A low peak, as in 1974, may indicate poor breeding compare with good breeding success as in 1975, and intermediate success as in 1973. Good breeding in 1975 may have been due to increased vertebrate mortality as a result of a cold spell from mid May to mid June, when temperatures of $-5^{\circ}C$ and heavy rainfall was recorded. It is known that a combination of high rainfall and low temperature causes mortality in nestling birds (Fox, 1976). Such weather conditions did not occur in 1974, and this may explain the poor breeding of Necrophorus in that year.

Fluctuations in numbers of second-generation adults is associated with variations in the size of the beetles fat reserves. When numbers were high, in 1973 and 1975, fat reserves at the end of the season were low. When numbers were low in 1974, fat reserves were high. The significance of this relationship cannot be deduced from field studies alone.

The population study unfortunately failed to answer a

fundamental question about the biology of burying beetles - do they breed more than once? It has usually been assumed (Pukowski, 1933; Springett, 1967; this study) that they breed only once. No evidence is available to prove or disprove this assumption. Some circumstantial evidence may, however, suggest that Necrophorus could breed more than once. Burying beetles can live a long time. Some marked individuals are known to have lived for more than 100 days. Two N.vespilloides from the breeding population survived overwinter (i.e. more than a year), and post reproductive N.investigator may also survive overwinter. As breeding only takes about 20 days, it may be asked why adults should survive for such a long time if they only breed once. Indeed the presence of eggs in post reproductive individuals would suggest that it might be necessary for some Necrophorus to breed more than once if they are to lay alltheir eggs. In the absence of further data, this must remain speculation. Only extensive marking and identification of the individuals burying particular corpses would suffice to clarify this matter in the field. In the laboratory, burying beetles could be offered very small corpses, allowed to breed, then offered a second corpse. This problem must be solved before the ecology of burying beetles can be completely understood.

The occurrence of particular species of burying beetles in different areas has been explained by some authors on the basis of habitat selection. Based on trapping records, preferences have been proposed for particular vegetation or soil (Table 2:12). No attempt was made by these authors to relate the presence of a particular species of burying beetle to the presence of suitable carrion. Differences in the density of birds are known to occur in different types of habitat (Table 2:13), and densities of small mammals will presumably differ in a similar way. If it is assumed that different densities of vertebrates will lead to differences in the amount of carrion available in different

Table 2:12.

Habitat preferences of *Necrophorus*

Species	Authority			
	Pukowski (1933)	Paulian (1946)	Canntonnet and Lecordier (1947)	Théorides (1950)
N.humator	Moist deciduous forests (damp conifer woods)	Thick heavy soils	Meadows, damp hollows in woodland	Damp woodland soil rich in humus
N.vespilloides	Dry coniferous woods (dry deciduous woods)	-	Dry mounds, damp hollows in woods, not in meadows	Woodland areas with sandy soil. Dry coniferous woods, very damp areas.
N.vespillo	Meadows	-	Meadows, damp hollows in woodland	Damp woods, damp meadows
N.vestigator	-	Poor dry soils, open terrain	Meadows, damp hollows of woodland	Meadows with dry soil, sunny barren areas.
N.germanicus	-	Thick, heavy soils	-	Damp woods soil rich in humus
N.interruptus	-	-	Damp hollows in woodland, not in meadows	Damp woodland soil rich in humus

Table 2:13.

Differences in bird densities in different habitats

Habitat	Location	Bird Density (prs/ha)	Author
Oak woodland	Loch Lomond:		
"	Inchcailloch west	15.05	Williamson (1972)
"	Inchcailloch east	11.90	"
"	Clairinsh	12.20	"
"	Torrinch	9.80	"
"	Creinch	7.80	"
"	Craigroyston	11.50	"
"	Arrochymore	11.54	Flegg and Bennett (1974)
"	7 woods, England (mean)	16.48	"
"	2 woods, Wales (mean)	4.53	"
"	Derrycunihy woods, Ireland	15.18	"
"	Wester Ross, Scotland	13	Williamson (1969)
Birch wood	Finland	6	Von Haartman(1971)
"	Wester Ross, Scotland	11	Williamson (1964)
Pine Wood	Finland	1	Von Haartman(1971)
"	Wester Ross, Scotland	2	Williamson (1969)
Pine and birch woods	Strathspey, Scotland	4	Newton and Moss (1977)

habitats, a more likely explanation for habitat selection by burying beetles can be proposed, i.e. the type and relative density of carrion present governs the occurrence of particular species of burying beetle.. Vegetation and soil may influence burying beetles indirectly through their effects on the vertebrates (Newton and Moss, 1977).

There is no evidence that habitat selection occurs on Inchcailloch, as all three species are found in the same habitat. Although more N.vespilloides were found on the west side of Inchcailloch than the east, perhaps associated with a denser bird population on the western side of the island, it is not possible to conclude that preferences were shown for areas within the island. In the first place, birds may provide a smaller proportion of the carrion than small mammals, and there is no data on the density of mammals. Secondly, preferences for areas within the island were not shown every year by N.vespilloides, and were not shown at all by the other two species. Thirdly, burying beetles are powerful fliers (Petrůska, 1964; Springett, 1967) and would be unlikely to limit themselves to one part of the island while searching for carrion.

If areas with different habitats and different densities and types of carrion are different in respect of the Necrophorus species present, it might be expected that the converse might be true, namely that areas with similar habitats and with similar corpse density and availability should have similar Necrophorus species. This has not been tested, but a preliminary examination of some species lists suggests that there may indeed be some evidence to support the hypothesis. Inchcailloch and Monks Wood, Huntingdon (Welch, 1973) are both oak woods, with a wide range of small mammals and birds (Mellanby, 1973). N.vespilloides, N.humator and N.investigator are the burying beetle species found in both areas. Inner Farne island, Northumberland

(Springett, 1967) and Skomer, Pembrokeshire (Sage, 1977) are both offshore, treeless islands where seabirds are the main source of carrion. N.investigator and N.humator are the only burying beetles present. Although small mammals, notably the Skomer vole, are present on Skomer, they do not breed until June (Jewell, 1965, 1966; Rowlands, 1969) and predation is very heavy (Plant, 1970). They would therefore be unavailable for a burying beetle breeding in April and May.

Consideration of the corpses available and their density may explain the discontinuous distribution of Necrophorus species in Britain. The relative abundance of species in particular areas may also be explained in this way. N.vespilloides, for example, is more abundant on Inchcailloch than N.investigator. This may be associated with a greater availability of corpses when N.vespilloides is breeding. Differences may exist between N.vespilloides populations on Inchcailloch and the mainland. The absence of a second peak of N.vespilloides on the mainland suggests that breeding is poor in this area, and this is supported by the greater turnover in the population on the mainland. An explanation for poorer breeding on the mainland could be a shortage of suitable corpses due to differences in habitat from Inchcailloch, greater human activity and the presence of scavengers such as buzzards (Buteo buteo L.), foxes (Vulpes vulpes L.) and badgers (Meles meles L.). Interpretation of results to explain the relative abundance of species on this basis must be carried out carefully however. N.humator appears to be the least numerous species on Inchcailloch. It is, however, abundant under large corpses. There appears to be a low population because the trap used is unsuitable. Only species with the same type of corpse preference can be compared using trapping data alone.

SECTION 3.

INTERSPECIFIC COMPETITION FOR CARRION

3. INTERSPECIFIC COMPETITION FOR CARRION

3.1. Introduction

The relationships between the three species of Necrophorus in the study area were analysed to explain how they might coexist. Particular attention was paid to the breeding seasons of the three species. Intense intraspecific competition for corpses on which to breed has been demonstrated by Fabre (1919), Pukowski (1933) and Springett (1967). Competition between species might be expected at this time. The main aim of the experiments, therefore, was to find out if interspecific competition for corpses occurred during the breeding seasons of the three species.

The definition of competition to be used is that suggested by Klomp (1964) : "Competition occurs when two or more organisms exert disadvantageous influences upon each other, because their demands exceed the immediate supply of a common resource". In this instance, the common resources being competed for are corpses for breeding. To show that competition was occurring, it was considered necessary to demonstrate that one species was interfering with the breeding of another in some way. Three criteria were used to show this, namely :

a) The potential for competition must exist. Both species must be present at the same time, in breeding condition, and they must be shown to utilise the same resource during the same period.
b) The breeding performance of at least one of the species must be reduced in the presence of the other species.
c) In the absence of one of the species, the breeding performance of the other must be increased.

These criteria are similar to those used by Pontin (1961, 1963, 1969) to prove the occurrence of interspecific competition. The

proofs for the occurrence of competition as used by Reynoldson and Bellamy (1971), Lock and Bellamy (1976) were not considered relevant to this study as they required that species displacement occur in the field. Such displacement was considered unlikely over the short period of the study.

3.2. Materials and methods

3.2.1. Description of Study area.

To avoid interference with the population study on Inchcailloch experiments were initially carried out on the Ross Peninsula (NS 373960). This area was abandoned after the first year as a badger ate most of the corpses put out. All subsequent experimental work was carried out in the woodland of Rossdhu estate (NS 354873) (fig. 2:1). These woodlands are occasionally grazed by sheep and are consequently more open than those of Inchcailloch. Differences in the nature of the woodland were balanced by ease of access and the virtual absence of scavenging.

Only a small part of the woodland of Rossdhu estate (about 18 ha) was used in the study. The area resembles parts of Inchcailloch in many respects, but there are some differences. The area is fairly flat, nowhere above 50m, and boggy in places. The ground flora of the woodland is dominated by grasses such as Holcus lanatus L. and Deschampsia flexuosa L., with dense stands of bracken. Sphagnum mosses are found in the boggy areas. The birds and small mammals of the area have not been recorded, although rabbits (Oryctolagus cuniculus L.) and hedgehogs (Erinaceus europaeus L.) were both observed. A buzzard was seen on several occasions.

3.2.2. Scavenging activity in the study area.

Before experiments were carried out at Rossdhu, the loss of carrion to scavengers was assessed. 100 mouse and rat corpses were placed at random throughout the study area. The rear feet of the corpses were tied to canes with stout string. Corpses were examined daily during late July and August 1973, until they disappeared, dried up or were consumed by insects. Corpses which had been removed from the string were assumed to have been taken by bird or mammalian scavengers. The proportion of corpses taken by scavengers at Rossdhu was then compared with that from the Ross Point (Table 3:1). 90.56% of all corpses used at the Ross Point were removed by scavengers, while only 6% were removed at Rossdhu. This level of loss was considered acceptable, and it was decided to proceed with experiments at Rossdhu. During subsequent experiments at Rossdhu, only 13.56% of carrion was removed by scavengers (Table 3:2). It is probable that the main scavenger at Rossdhu was a buzzard.

3.2.3 Field Experiments

3.2.3.1. Experimental procedure.

Type of corpses used:

Mouse, rat and chick corpses were used, and stored deep frozen until required. Before use in the field, corpses were weighed and a numbered tag attached to the hind leg with string. The average weights of the corpses used in experiments is given in Table 3:3.

For experiments on corpse selection, the weight and volume of some corpses was altered. To retain the volume, while reducing weight (light mice, light rats), the corpse was dissected and the internal organs and ribcage removed. The skin was then sewn back together with waterproof nylon thread. To increase the weight of mice without

Table 3:1.

Loss of Carrion to Scavengers

	Type of carrion	Total number of corpses	Number removed by scavengers	% removed by scavengers
Ross Point (1973)	mice	160	157	98.13
	rats	20	6	30.00
	Total	180	163	90.56
Rossdhu (1973)	mice	80	4	5.00
	rats	20	2	10.00
	Total	100	6	6.00

Table 3:2.

Fate of Corpses during experiments at Rossdhu

(1974 - 1975)

	Number	% of total
Buried by *Necrophorus*	898	54.42
Removed by scavengers	224	13.57
Taken by other insects (e.g. Blowflies *Geotrupes*)	439	26.61
Untouched	89	5.39
Total number of corpses:	1650	

Table 3:3.

Size of carrion used in laboratory and field experiments (1974 - 1975)

Corpse	Number	Weight (gms) $\bar{x}$	SD	Approx. volume (cm^3)
mouse	2120	24.290	10.369	300
chick	170	44.80	12.606	455
rat	1034	289.80	80.797	2400
superchick (X4)	50	176.48	20.825	1900
supermouse (X4)	200	92.56	23.288	455
light rat	200	101.56	18.925	2400
heavy mouse	30	98.68	11.239	300
light mouse	30	11.22	4.621	300

altering volume (supermice), four or five mice were sewn tightly together with waterproof nylon thread. Alternatively, 75 gms lead shot was poured into the abdominal and thoracic cavity of a mouse, and the skin sewn back together (heavy mice). The weights of these abnormal corpses are shown in Table 3:3.

Naturally occurring carrion was examined whenever found at Rossdhu, Inchcailloch and the Ross Point. The corpses of deer, sheep, rabbits, squirrels and several types of bird were examined in this way. Dog corpses used for teaching purposes were also examined.

Use of corpses in the field.

Corpses were placed on the ground, about 12m apart, canes being used to mark the position of the corpse in the undergrowth. So that the corpse could be relocated after burial, the hindlegs were tied to the cane with about 1m of stout string. As far as possible, different parts of the study area were used for different experiments.

Examination of corpses.

During an experiment, corpses were examined as often as was practical, usually 2-3 times per week. If burial had occurred, the corpse was dug up and the species of Necrophorus responsible for burial recorded. If required for further experiments, the corpse was reburied.

3.2.3.2 Description of Experiments

The purpose of the field experiments was to test if beetles showed any preference for particular types of corpse. Records of which beetles buried the corpses in relations with resources experiments were used to determine the potential for competition at different times of the year.

a) Potential for competition

Mouse and rat corpses were randomly assigned to positions on a grid. 860 corpses were used in 1974 and 790 in 1975, in the experiments described in 4.2. The proportion of corpses buried and the species of beetle involved were recorded from April to September 1974 and from April to August 1975. For analysis, burial of corpses was split into three periods: April to mid-June, when N. vespilloides only was present, mid-June to mid-August, when both N. vespilloides and N. investigator were present, and mid-August to September, when N. investigator only was present.

Firstly the records for 1974 and 1975 were combined to determine the extent to which the two species buried corpses at the same time, and whether there was any difference between the proportion of corpses buried by each species when on its own, and in the presence of the other.

Secondly, burial of mice and rats was considered to find out if the beetles showed any preference for particular types of corpse. These results were used for comparison with those of the corpse selection experiments described below.

b) Corpse Selection

Two series of experiments were carried out to test for corpse selection. In the first, mice and rats were used, placed alternately on a grid. Groups of mice only and rats only were used as controls. A total of 135 mice and 105 rats were used in experimental groupings in 1974, with 220 mice and 115 rats as controls. 80 mice and 70 rats were used in experiments in 1975, with 50 mice and 40 rats as controls. Experiments were repeated three times, April to mid-June, mid-June to mid-August and mid-August to September, in order to obtain each beetle species separately and the two species together. The results

of these experiments were not combined with those of the previous experiments because the method of putting out corpses was different - corpses were placed alternately to give beetles some choice, while in the monitoring experiments, corpses were set out randomly.

In the second series of corpse selection experiments, abnormal corpses were used. Two types of corpse were paired together, tied to the same cane. Pairs used were:- mice / chicks, mice /supermice, supermice / light rats and light rates / rats. Supermice, light rats, heavy mice and light mice were put out in groups on their own as controls. The number of corpses used is given in tables 3:17 and 3:18. Results of these experiments were also used in section 4.

3.2.4. Laboratory Experiments

3.2.4.1. Experimental procedure

Collection and storage of beetles.

Burying beetles for laboratory experiments were collected from the Ross point when required, using the same trap as used in the population study (fig. 2:5). Beetles were used for experiments as soon after capture as possible. If necessary, beetles were stored in

2 lb Kilner jars with air holes punched in the lid, and 2-3 inches of soil and leaf litter in the bottom of the jar. A maximum of 10 N.vespilloides or 5 N.humator/N.investigator were kept in each jar. Normally no food was given to the insects during storage, although if beetles were to be kept longer than 3-4 days, small pieces of meat were put in the jar as food.

Storage jars were kept in an insectary under normal daylight conditions. Care was taken to keep the jars shaded and out of direct sunlight. The soil in the jars was kept moist, as beetles proved sensitive to high temperatures and desiccation. Beetles were released at the Ross Point when no longer required.

Experimental conditions.

Experiments were normally carried out in insectaries. Temperatures varying through the normal daily range appeared to have no effect on the actions of beetles in experiments. Care was taken, however, to keep experimental containers out of direct sunlight. Temperatures were monitored and beetles were removed from the insectaries if temperatures rose above 30°C.

When experiments were carried out in the laboratory, beetles were allowed to acclimatise to any changes in conditions for one hour before experiments were carried out. This was probably unnecessary as there were no apparent differences in behaviour between insectary and laboratory.

Experiments on competition were usually carried out during the day. Experiments carried out at night took place either in the dark or under fluorescent lighting. Burying beetles were observed to bury carrion, if offered, at any time of the day or night, and burial appeared

to be equally successful during day or night, in light or darkness.

Experimental containers.

Burial experiments were normally carried out in plastic plant germinating trays (30cm x 65cm x 5cm), filled to the brim with soil. The holes in the bottom of the trays were sealed with adhesive tape to prevent escapes. Leaf litter was scattered over the soil surface. The trays were covered with clear perspex covers (25cm high), and the adjustable ventilators in the top of the cover were left slightly open. Experiments were sometimes carried out in wooden framed gauze cages (30cm x 30cm x 30cm). Soil to depth of about 8cm covered the bottom and leaf litter was scattered on top of the soil. Although these cages were more convenient for handling and storage, their use was discontinued as beetles were able to chew through the gauze and escape.

3.2.4.2. Description of Experiments

The aim of these laboratory experiments was to determine whether the two species competed for corpses or showed any preference for corpses.

a). Competition for Corpses.

Two experiments were carried out to test for competition between N. vespilloides and N. investigator, and for comparative purposes, results on the proportion of corpses buried by each species on its own obtained in experiments described in section 4 were also used. 1370 mouse and rat corpses were offered to N. vespilloides in various breeding and mortality experiments in 1973, 1974 and 1975. 500 were offered to N. investigator. The proportion of corpses buried provided a figure for burial of corpses by each species on its own in the laboratory. These experiments were carried out from April to mid-June and mid-August to September.

Burial of corpses when two species were present was tested in two experiments.

A male / female pair of both N. vespilloides and N. investigator were introduced into the experimental chamber at the same time. The species responsible for burial was recorded. Experiments were carried out from mid-June to mid-August when breeding N. vespilloides and N. investigator were available. 150 corpses were used in three replicates of 150 in 1974, and 100 in two replicates of 50 in 1975. As control, in 1974, 50 corpses were offered to N. vespilloides and N. investigator on their own. These results were compared with the proportion buried by each species on its own ealier and later in the year, and were not included in overall records of burial by each species on its own.

In a second series of experiments, N. investigator pairs were added to corpses 24 hours after N. vespilloides were added, to test if there was any interference during burial. These experiments were carried out in July 1975, and 109 mouse corpses were used.

b). Preferences for Corpses

Selection experiments carried out in the laboratory were designed to test the preferences of beetles when offered a choice of corpses.

Two corpses were placed in an experimental container at the same time. Each corpse was placed 8cm from the edge. A pair of burying beetles was then introduced into the container, or two pairs if two species were to be tested at the same time. As controls, single corpses were placed in the centre of the container.

In one series of experiments, normal mice and rats were used. Experiments were carried out three times - April to mid-June, mid-June to mid-August and mid-August to September, to test the preferences of N. vespilloides, N. vespilloides and N. investigator together and

N. investigator respectively. For N. vespilloides on its own, 23 mouse / rat pairs were used in 1974, with 50 in 1975. 50 individual mice and 30 rates were used as controls in 1974. For N. vespilloides and N. investigator together, 25 mouse / mouse pairs were used, together with 20 individual mice and 20 rats as controls. This was carried out only in 1974. The preferences of N. investigator on its own were also tested in 1974 only, using 50 mouse / rat pairs, and 50 individual mice and 25 chicks as controls.

In a second experiment, pairs of abnormal corpses were used, in an attempt to determine the mechanism beetles use to select a particular type of corpse. These experiments were carried out from April to mid-June and mid-August to September 1974, and used each beetle species on its own. Corpse pairings used were : mice / chicks, mice / supermice, supermice / light rats, light rats / Rats. The number of corpses used is given in tables 3:17 and 3:18.

3.3. Results

3.3.1. The evidence for Interspecific Competition.

3.3.1.1. The presence of adult beetles.

Interspecific competition for corpses can only occur if adult beetles are present to bury the corpses. Both N.vespilloides and N.investigator were present from the beginning of July to mid September 1973, the end of July to the end of August 1974 and during July 1975 (figs. 2:10 - 2:12, 2:19 - 2:24). N.humator adults were present at the same time as those of N.vespilloides. These observations suggest that at certain times of the year, mature adults of the three species are present together on Inchcailloch.

3.3.1.2. Burial of corpses.

Adults must not only be presemt at the same time, but must use the same resource. If the beetles bury different types of corpse, interspecific competition may be avoided.

During the period June to August 1974, and June to July 1975,

N.vespilloides and N.investigator both buried experimental corpses (Table 3:4). This suggests that both species are burying the same type of corpse at the same time. N.humator, however, buried less than 1% of the corpses used in experiments (Table 3:4). Further, N.humator was not recorded during extended observation of the burying beetles arriving at small corpses. Investigation of large carrion showed that N.humator was very common under this type of corpse (Table 3:5). Most N.humator appear to exploit large carcasses, and do not bury small corpses used by N.vespilloides and N.investigator. There is, apparently, little potential for interspecific competition between N.humator and the other two species, and so N.humator is not considered further in this analysis.

3.3.1.3. Proportions of corpses buried.

The number of corpses buried by N.vespilloides and N.investigator was examined, in the absence of the other species and when it was present. The two species were considered as being present together at Rossdhu from mid June to mid August. Breeding N.vespilloides alone occur from April to mid June, while breeding N.investigator occur on their own from mid August to September.

During 1974, 60% of the corpses put out in the field were buried by N.vespilloides in the absence of N.investigator, and 56.7% in 1975 (Table 3:6). The corresponding figures for burial by N.investigator in the absence of N.vespilloides are 62% in 1975 and 8.9% in 1974. The proportion of corpses buried by N.vespilloides is not significantly different between years, nor is it significantly different from that buried by N.investigator in 1975. Burial by N.investigator in 1974 is, however, significantly different from that by both N.investigator and N.vespilloides in 1975. The low number of corpses buried by N.investigator

Table 3:4.

Burial of corpses by Necrophorus Monthly Distribution.

Month	Total number corpses	Corpses buried Number	% of total	Corpses buried by N.vespilloides Number	% of total buried	N.investigator Number	% of total buried	N.humator Number	% of total buried
1974									
April	120	61	50.93	60	98.36	0	0.00	1	1.64
May	200	143	71.5	143	100.00	0	0.00	0	0.00
June	220	136	61.82	123	90.44	13	9.56	0	0.00
July	100	45	45.00	0	0.00	42	93.33	3	6.67
August	120	41	34.17	8	19.51	33	80.49	0	0.00
September	100	0	0.00	0	0.00	0	0.00	0	0.00
Total 1974	860	426	49.53	334	78.40	88	20.66	4	0.94
1975									
April	100	2	2.00	1	50.00	0	0.00	1	50.00
May	220	147	66.82	146	99.32	0	0.00	1	0.68
June	200	160	80.00	141	88.12	18	11.25	1	0.63
July	150	86	57.33	4	4.65	82	95.35	0	0.00
August	120	77	64.17	0	0.00	77	100.00	0	0.00
Total 1975	790	472	59.75	292	61.86	177	37.50	3	0.64
Total (both years)	1650	898	54.42	626	69.71	265	29.51	7	0.78

Table 3:5.

The number of Necrophorus observed on large carrion examined at Rossdhu and the Ross Point.

Type of Corpse	Number examined	Number of Necrophorus			
		N.vespilloides	N.investigator	N.humator	(Necrodes littoralis)
Deer	2	6, 8	0, 0	20,* 15*	(50,* 20*)
Sheep	3	5, 4, 10	0, 0, 0	50,* 100,* 50	(50,* 100,* 30)
Rabbit	1	6	0	3	0
Squirrel	1	0	0	0	0
Dog	4	3, 0, 2, 1	0, 0, 0, 0	25,* 30,* 12,* 18	(10,* 30,* 15,* 15*)

(* Approximate figures)

Table 3:6.

Burial of corpses in the field by Necrophorus

N.vespilloides alone (April to mid June)

Year	Number of corpses	Corpses buried by N.vespilloides Number	%
1974	470	284	60.43
1975	430	244	56.74
Total	900	528	58.67

(χ^2 = 0.327 d.of f. 1 $p > 0.05$)

N.investigator alone (mid August to September)

Year	Number of corpses	Corpses buried by N.investigator Number	%
1974	180	16	8.89
1975	85	53	62.35
Total	265	69	26.04

(χ^2 = 45.79 d.of f. 1 $p < 0.001$)

Comparison of ratio of corpses buried to corpses put out

1974 N.vespilloides - N.investigator $\chi^2 = 56.97$ d.of f. 1 $p < 0.001$

1975 N.vespilloides - N.investigator $\chi^2 = 0.240$ d.of f. 1 $p > 0.05$

in 1974 may have been due to the low numbers of this species in the area at the time (c.f. fig. 2:11). High rainfall during this period (fig. 2:3 and Table 2:11) waterlogged corpses and the soil and may also have affected corpse burial.

These results suggest that both N.vespilloides and N.investigator may bury similar proportions of corpses when the other species is absent, unless other factors affect burial. This hypothesis is supported by laboratory experiments. 92.5% of the corpses offered to N.vespilloides on its own were buried and 81.8% of those offered to N.investigator (Table 3:7). These proportions are not significantly different.

The difference between proportions of corpses buried in field and laboratory is significant both for N.vespilloides ($\chi^2 = 46.22$, d.of f. 1, $p < 0.001$) and N.investigator ($\chi^2 = 61.12$, d.of f. $p < 0.001$). A higher proportion of corpses is buried in the laboratory as scavengers and arthropod predators are absent and no long range searching for corpses is required. Such a high rate of burial is unlikely ever to occur in the field.

When N.vespilloides and N.investigator are both present, the overall proportion of corpses buried does not change. In the field 61.4% of corpses were buried by the two species combined (Table 3:8). This is not significantly different from the proportion buried by N.vespilloides on its own (1974, $\chi^2 = 0.003$, d.of f. 1 , $p > 0.05$; 1975, $\chi^2 = 0.833$, d.of f. 1, $p > 0.05$), or by N.investigator on its own (1975, $\chi^2 = 0.010$, d.of f. 1, $p > 0.05$). Burial of corpses by N.investigator in August 1974 was considered abnormal and not compared. 21% of corpses were buried by N.vespilloides and 40.4% by N.investigator (Table 3:8). These proportions are significantly different from those observed when the species are on their own (Table 3:9). The proportion

Table 3:7.

Burial of corpses by *Necrophorus* in the laboratory

N.vespilloides only

Year	Number of corpses offered	Number of corpses buried	% Corpses buried
1973	370	322	87.03
1974	750	720	96.00
1975	250	226	90.40
Total	1370	1268	92.55

N.investigator only

Year	Number of corpses offered	Number of corpses buried	% corpses buried
1973	150	122	81.33
1974	250	193	77.20
1975	100	94	94.00
Total	500	409	81.80

Difference in proportion of corpses buried by *N.vespilloides* and *N.investigator* (totals) not significant

$\chi^2 = 2.560$ d. of f. 1 $p > 0.05$.

Table 3:8.

Burial of corpses by Necrophorus in the field.

Both species present (Mid June - Mid August)

	1974		1975		total	
	Number corpses buried	% buried	Number buried	% buried	Number buried	% buried
Total Corpses buried	123	58.57	175	63.64	298	61.44
Corpses buried by *N.vespilloides*	51	24.29	51	18.55	102	21.03
Corpses buried by *N.investigator*	72	34.28	124	45.09	196	40.41
Total corpses put out	210		275		485	

Table 3:9

Burial of corpses by Necrophorus in the field: Comparison of burial in the presence and absence of the other species.*

Burial of Corpses by N.vespilloides

	1974		1975	
	Number of corpses		Number of corpses	
	Unburied	Buried	Unburied	Buried
Absent	186	284	186	244
N.investigator				
Present	159	51	224	51
	χ^2= 75.85 doff 1	p<0.001	χ^2= 100.5 doff 1	p<0.001

Burial of Corpses by N.investigator

	1974		1975	
	Number of corpses		Number of corpses	
	Unburied	Buried	Unburied	Buried
Absent	164	16**	32	53
N.vespilloides				
Present	138	72	151	124
	χ^2= 35.78 doff 1	p<0.001**	χ^2= 7.74 doff 1	p<0.01

* Data from Table 3:6.

** Burial by N.investigator in August 1974 is believed to be unusual.

of corpses buried by each species is reduced when the other is present.

This hypothesis is supported by laboratory evidence. When pairs of the two species were added to a corpse at the same time, N.vespilloides buried only 0.4% of corpses, compared with 90.4% buried by N.investigator (Table 3:10). In a control experiment, pairs of N.vespilloides and N.investigator were added to corpses separately, and buried 54% and 92% of corpses respectively. In the laboratory, the proportion of corpses buried by N.investigator in the presence of N.vespilloides is not significantly different from that buried in its absence (this experiment, $\chi^2 = 0.010$, d.of f 1, $p > 0.05$; comparison with previous experiment, Table 3:7, $\chi^2 = 0.708$, d.of f 1, $p > 0.05$). N.vespilloides buried almost no corpses when N.investigator was present in the laboratory. Even in the absence of N.investigator, N.vespilloides buried a significantly smaller proportion of corpses than it did earlier in the year (Table 3:7) ($\chi^2 = 5.070$, d.of f. 1, $p < 0.05$). This may be due to the declining number of mature individuals in the population at this time of year (c.f. figs. 2:19 - 2:21). Part of the reduction in burial observed in the presence of N.investigator may be due to the reduction in number of mature N.vespilloides. This is not the only reason, however, as some mature individuals are still present. Dissection of 50 N.vespilloides trapped at Rossdhu at this time of year showed that 24 (48%) were mature. Therefore the low rate of burial by N.vespilloides must be due to the presence of N.investigator.

When N.vespilloides and N.investigator were together on a corpse, stridulation was heard, and it was assumed that direct interference by N.investigator was occurring. This was not observed however, as any fighting took place underground. Indirect evidence for interference comes from experiments in which N.investigator was not added to the container until 24 hours after the addition of N.vespilloides. 52% of

Table 3:10

Burial of Corpses by Necrophorus in the laboratory. Corpses offered to N.vespilloides and N.investigator together

Year	Number of Corpses offered	Total buried		Buried by N.vespilloides		Buried by N.investigator	
		No.	%	No.	%	No.	%
1974	150	136	90.67	0	0.00	136	90.67
1975	100	90	90.00	1	1.00	89	89.00
Total	250	226	90.4	1	0.40	220	90.00

Difference between N.investigator 1974 and 1975 ratios not significant.

$\chi^2 = 0.010$ doff 1 $p > 0.05$

Corpses offered to N.vespilloides and N.investigator individually (1974 only)

Species	Number of Corpses offered	Number buried	% buried
N.vespilloides	50	27	54.00
N.investigator	50	46	92.00

the 109 corpses used were buried by N.vespilloides within 24 hours (Table 3:11). This is not significantly different from the proportion of corpses buried by N.vespilloides in the absence of N.investigator at this time of year (Table 3:10) ($\chi^2 = 0.179$, d.of f. 1, $p > 0.05$). None of the corpses buried by N.vespilloides were subsequently taken over by N.investigator, although 79% of the remaining corpses were buried by this species. This is not significantly different from the proportion of corpses buried by N.investigator in the absence of N.vespilloides (Table 3:10) ($\chi^2 = 0.279$, d.of f. 1, $p > 0.05$). These results show that as long as N.vespilloides succeeds in burying a corpse, it is not affected by the subsequent presence of N.investigator. Only if N.investigator is present during burial is there a reduction in the number of corpses buried by N.vespilloides.

3.3.1.4. Evidence from the population study.

Each year, the emergence and first breeding of N.investigator is followed a month later by the end of the breeding of N.vespilloides (fig. 2:19 to 2:24). The reasoning behind these estimates is set out in 2.3.1.5. In both 1973 and 1975, N.investigator emerged and bred at the beginning of July and N.vespilloides appeared to stop breeding at the end of July. Mature N.vespilloides were still present in September 1973 however (fig. 2:19). In 1974, N.investigator emerged in mid July (Table 2:4) and did not breed until the end of July, nearly a month later than in 1973 and 1975. It is estimated that N.vespilloides bred for the last time at the end of August in 1974, also a month later than in the other two years. There is no direct evidence that the absence of N.investigator allows N.vespilloides to breed. The results do suggest, however, that when N.investigator is absent, N.vespilloides can breed later in the season than normal.

Table 3:11

Burial of Corpses by *Necrophorus* in the laboratory.

(*N.investigator* added 24 hours after *N.vespilloides*)

	Number	%
Corpses used	109	
Buried by *N.vespilloides* after 24 hours	57	52.29
Unburied	52	
Unburied corpses ultimately buried by *N.investigator*	41	78.84
Corpses buried by *N.vespilloides* and subsequently taken over by *N.investigator*	0	0

On the mainland, N.investigator appears to emerge earlier than on Inchcailloch (Table 2:2); corpses are buried at Rossdhu in June by N.investigator (Table 3:4). In 1975, no burials by N.vespilloides are observed after July, about a month after the first burials by N.investigator. In 1974, however, N.vespilloides buries corpses during June, July and August, despite the presence of N.investigator. This longer period of coexistence may be associated with low numbers of N.investigator in the study area. (c.f. the low number of corpses buried by N.investigator in 1974, Table 3:6, and low numbers in the mainland and Inchcailloch traps, figs. 2:10 to 2:13) as well as the later emergence of N.investigator in 1974.

3.3.2. Evidence that interspecific competition is avoided.

In 3.3.1.2. it was observed that both N.vespilloides and N.investigator buried rats and mice, while N.humator did not. If a preference for either rats or mice could be demonstrated in N.vespilloides or N.investigator, the potential for competition would be removed. The existing data was analysed to test if there was any difference in the proportion of each type of corpse buried. Experiments were then carried out to test if any preference for corpses was shown when a choice was available.

3.3.2.1. Further analysis of existing results.

Similar proportions of mice and rats are buried by each species when on its own in 1974 (Table 3:12). In 1975, significantly more mice than rats were buried by N.vespilloides on its own, and significantly more rats than mice by N.investigator. This was also observed, in both years, when the two species were together. Interpretation of these results is complicated by the reduction in the number of corpses buried

Table 3:12.

Burial of different types of corpse in the field by Necrophorus

(Reanalysis of data in Table 3:6).

	Necrophorus species present							
	N.vespilloides				N.vespilloides N.investigator			
	Number of corpses out	unburied	buried	% buried	Number of corpses out	unburied	buried	% buried
1974 N.vespilloides								
mice	320	131	189	59.06	140	139	51	36.43
rats	150	55	95	63.33	70	70	0	0.00
	χ^2	0.779	p > 0.05		Not calculated			
N.investigator								
mice					140	114	26	18.57
rats					70	24	46	65.71
					χ^2	46.03	p < 0.001	
1975 N.vespilloides								
mice	315	124	191	60.63	195	146	49	25.13
rats	115	62	53	46.09	80	78	2	2.5
	χ^2	7.26	p < 0.01		Not calculated			
N.investigator								
mice					195	134	61	31.28
rats					80	17	63	78.75
					χ^2	51.62	p < 0.001	

	N.investigator							
	Number of corpses out	unburied	buried	% buried				
1974 N.vespilloides								
mice	150	138	12	8.00				
rats	30	26	4	13.33				
	χ^2	0.878	p > 0.05					
1975 N.vespilloides								
mice	55	28	27	49.09				
rats	30	4	26	86.67				
	χ^2	12.9	p < 0.001					

by both N.vespilloides and N.investigator in the presence of the other species. N.vespilloides buries a significantly smaller proportion of mice when N.investigator is present (1974, $\chi^2 = 49.63$, d.of f. 1, $p < 0.001$; 1975, $\chi^2 = 60.95$, d.of f. 1, $p < 0.001$), while the number of rats buried is greatly reduced. N.investigator buries significantly fewer mice when N.vespilloides is present (1974, $\chi^2 = 7.11$, d.of f. 1, $p < 0.01$; 1975, $\chi^2 = 5.96$, d.of f. 1, $p < 0.05$). The proportion of rats buried in the presence of N.vespilloides does not change however (1975, $\chi^2 = 0.885$, d.of f. 1, $p > 0.05$; 1974, not calculated).

These results suggest that N.vespilloides may exhibit a preference for mice and N.investigator for rats, although both types of corpse are buried by both species of beetle. When the two beetle species are present together, the apparent preference is enhanced, as N.vespilloides does not bury any rats, while the proportion of mice buried by N.investigator is also reduced.

3.3.2.2. Experimental analysis of corpse selection

Pairs of mice and rats were used to test the preferences of N.vespilloides and N.investigator. Single mice, chicks and rats were used as controls. N.vespilloides on its own showed no preference for mice over rats, even when a choice was presented (Table 3:13). These observations confirm the preliminary findings of 1974, but disagree with those of 1975. N.investigator on its own buried a significantly higher proportion of rats, both when mixed and single types of corpse were offered. This agrees with the preliminary findings for 1975, but disagrees with those of 1974. These observations were tested further in the laboratory. Single pairs of either N.vespilloides or N.investigator were presented with a rat and mouse in the same container. As controls, other pairs of beetles were presented with single types of

Table 3:13.

Burial of different types of corpses by Necrophorus in the field

Type of corpse		Number of corpses put out	unburied	buried	% buried
N.vespilloides only (April to mid June)					
Pairs of corpses					
1974	mice	25	9	16	64.00
	rats	25	12	13	52.00
		χ^2 = 0.739	doff 1	p > 0.05	
1975	mice	50	22	28	50.00
	rats	50	27	23	50.00
		χ^2 = 1.00	doff 1	p > 0.05	
Single corpses					
1974	mice	50	15	35	70.00
	mice	30	15	15	50.00
	(chick	50	23	27	54.00
	mice : rats	χ^2 = 3.20	doff 1	p > 0.05	
N.investigator only (Mid August to September)					
(1974)					
Pairs of corpses					
	mice	50	44	6	12.00
	rats	50	27	23	46.00
		χ^2 = 14.04	doff 1	p < 0.001	
Single corpses					
	mice	50	35	15	30.00
	rats	25	11	14	56.00
	(chicks	25	21	4	16.00)
	mice : rats	χ^2 = 4.75	doff 1	p < 0.05	

corpse. N.vespilloides buried significantly more mice than rats when offered pairs of corpses (Table 3:14) and with single corpses in 1975. In 1974, however, the proportion of single mice and rats buried is not significantly different. N.investigator buried significantly more rats than mice when given a choice, and buried the same proportion of mice and rats when offered no choice.

The results for burial by each species on its own are, therefore, somewhat contradictory. In some cases a preference was shown, in others none. The only conclusion to be drawn is that when no choice is offered, N.vespilloides and N.investigator will bury both rats and mice. When a choice is offered, N.investigator will bury both rats and mice, while N.vespilloides sometimes shows a preference for mice and sometimes shows no preference.

These experiments were repeated when both species of Necrophorus were present together and led to similar conclusions. When no choice of corpse was offered in the field, both types of corpse were buried by both species (Table 3:15). As observed previously, N.vespilloides buried a significantly smaller proportion of mice ($\chi^2 = 102.95$, d.of f. $p<0.001$) and rats ($\chi^2 = 76.15$, d.of f. 1, $p<0.001$) than did N.investigator. When a choice of corpse was available, N.investigator buried rats and some mice, N.vespilloides mice and no rats. The proportion of mice buried by N.vespilloides was not significantly different from that buried by N.investigator ($\chi^2 = 1.62$, d.of f. 1, $p>0.05$). This confirms the earlier observation that when a choice of corpses is available, and both species are present, N.investigator prefers rats, but will also bury some mice. When there is no choice both mice and rats are buried equally. In the presence of N.investigator, N.vespilloides buries no rats and reduced numbers of mice. In the

Table 3:14.

Burial of different types of corpse by Necrophorus in the laboratory

Type of corpse		Number of corpses put out	unburied	buried	% buried
N.vespilloides only					
Pairs of corpses					
1974	mice	50	4	46	92.00
	rats	50	49	1	2.00
1975	mice	30	6	24	80.00
	rats	30	28	2	6.67
Single corpses					
1974	mice	15	1	14	93.33
	rats	15	5	10	66.67
	(chicks	10	2	8	80.00)
	mice : rats	$\chi^2 = 3.33$	doff 1	$p > 0.05$	
1975	mice	50	4	46	92.00
	rats	30	10	20	66.07
		$\chi^2 = 8.33$	doff 1	$p < 0.01$	
N.investigator only (1974)					
Pairs of corpses					
	mice	50	48	2	4.00
	rats	50	14	36	72.00
Single corpses					
	mice	50	19	31	62.00
	rats	30	8	22	73.33
		$\chi^2 = 1.08$	diff 1	$p > 0.05$	

Table 3:15

Burial of different types of corpse by Necrophorus vespilloides and N.investigator in the field

Type of corpse		Number of corpses	Corpses buried by N.vespilloides No.	%	N.investigator No.	%	Total corpses buried No.	%
Single corpses								
mice	1974	120	5	4.17	60	50.00	65	54.17
	1975	50	2	4.00	32	64.00	34	68.00
	Total	170	7	4.12	92	54.12	99	58.24
rats	1974	60	1	1.67	32	53.33	33	55.00
	1975	40	0	0.00	25	62.50	25	62.50
	Total	100	1	1.00	57	57.00	58	58.00
Mixed corpses								
mice)	1974	60)	8)	13.33)	11)	18.33)	19)	31.67)
rats)		35)	0)	0.00)	18)	51.43)	18)	51.43)
mice)	1975	30)	2)	6.67)	5)	16.67)	7)	23.33)
rats)		20)	0)	0.00)	13)	65.00)	13)	65.00)
mice)	Total	80)	10)	11.11)	16)	17.78)	26)	28.89)
rats)		55)	0)	0.00)	31)	56.36)	31)	56.36)

Differences between years not significant at p = 0.05

laboratory, pairs of rats and mice, pairs of mice, single rats and single mice were used to test the preferences of pairs of N.vespilloides and N.investigator. When pairs of rats and mice were buried, the rats were buried only by N.investigator, and the mice mainly by N.vespilloides (Table 3:16). Equal proportions of mice were buried by both species when mouse pairs were used. When single corpses were used, only N.investigator was successful. These results support the hypothesis that N.investigator prefers rats, and suggest that only when N.investigator has a chance to exercise a preference will N.vespilloides be able to bury any remaining corpses in the vicinity.

By using pairs of abnormal corpses, differing in weight and volume, an attempt was made to assess how many corpse selection might work. The weights and volume of the various type of abnormal corpses are shown in Table 3:3. In those cases where numbers are large enough to test, N.vespilloides buried similar proportions of corpses despite their differences in weight or volume (Table 3:17). In the combination of corpses with the same volume but different weights (mice - supermice, light rats - rats) N.investigator buried significantly higher proportions of the heavier corpses (Table 3:18). This result might suggest that weight may be involved in corpse selection but the number of replicates is too small to draw firm conclusions.

3.4. Discussion

Evidence that interspecific competition may occur between the burying beetles on Inchcailloch is summarised in Table 3:19. The possibility of competition between Necrophorus species has been considered in the past, and several methods whereby competition might be avoided have been proposed. Pukowski (1933), Paulian (1946), Cantonnet and

Table 3:16

Burial of different types of corpse by Necrophorus vespilloides and N.investigator in the laboratory.

(1974 only)

Type of corpse	Number of corpses offered	Corpses buried by * N.vespilloides No.	%	N.investigator No.	%	Total buried No.	%
Single corpses							
mouse	20	0	0.00	17	85.00	17	85.00
rat	20	0	0.00	13	65.00	13	65.00
Pairs of corpses							
mice	25	18	72.00	21	84.00	18	72.00
mice	25					21	84.00
mouse	30	21	70.00	1	3.33	22	73.33
rat	30	0	0.00	24	80.00	24	80.00

* One pair of both species present in the container at the same time

Table 3:17

Burial of different types of abnormal corpse by Necrophorus vespilloides

Type of Corpse	Field (mixed group)				Laboratory (pairs of mice)			
	Number of corpses offered	Number unburied	Number buried	% buried	Number of corpses offered	Number unburied	Number buried	% buried
mice	20	6	14	70.00	25	13	12	48.00
chicks	20	8	12	60.00	25	16	9	36.00
mice	25	9	16	64.00	10	4	6	60.00
supermice	20	6	14	56.00	10	8	2	20.00
supermice	15	11	4	26.66	20	14	6	30.00
light rats	15	9	6	40.00	20	12	8	40.00
light rats	20	13	7	35.00	15	10	5	33.33
rats	30	19	11	36.67	15	12	3	20.00
supermice	25	14	11	44.00				
light rats	15	8	7	46.67				
heavy mice	20	15	5*	25.00				
light mice	20	8	12	60.00				

* All corpses abandoned less than one week after burial.

Table 3:18

Burial of different types of abnormal corpse by *Necrophorus investigator*

Type of Corpse	Field (mixed group)				Laboratory (pairs of mice)			
	Number of corpses offered	Number unburied	Number buried	% buried	Number of corpses offered	Number unburied	Number buried	% buried
mice	20	6	14	70.00	20	10	10	50.00
chicks	20	10	10	50.00	20	12	8	40.00
mice	25	17	8	32.00**	15	13	2	13.33
supermice	25	8	17	68.00	15	8	7	46.67
supermice	20	5	15	75.00	21	15	6	28.57
light rats	20	7	13	65.00	21	13	8	38.09
light rats	15	9	6	40.00**	20	17	3	15.00**
rats	15	3	12	80.00	20	12	8	40.00
supermice	20	6	14	70.00				
light rats	15	4	11	73.33				
heavy mice	10	4	6*	60.00				
light mice	10	none buried						

* All corpses abandoned less than one week after burial

** $p < 0.05$

Table 3:19

Evidence for the occurrence of interspecific competition between N.vespilloides and N.investigator

1. Both species occur in the same place, at the same time of year.
2. Both species bury corpses at the same time of year.
3. Although corpse selection by N.investigator may occur, it is not completely effective in the field. In any event, the type of corpse preferred by N.investigator is absent from the study area. Both species bury the same types of corpse.
4. The appearance of N.investigator is correlated with the end of breeding of N.vespilloides
5. The proportion of corpses buried by each species is reduced when the other species is present.

Lecordier(1947) and Théorides (1950) suggest that interspecific competition is avoided by the selection of different habitats by different species. Trapping records however, show that Necrophorus vespilloides, N.humator and N.investigator are found in the same habitat in the study area. Novák (1964a, b) and Springett (1967) consider that species living in the same area may coexist by having different life cycles. N.vespilloides and N.investigator have different life cycles, but trapping results show that there is an overlap in breeding periods. Although for much of the breeding period each species is on its own, mature individuals of both species may occur at the same time, over a period of about one month. N.humator has the same breeding period as N.vespilloides. Therefore, neither habitat selection or differences in life cycles are effective methods of preventing interspecific competition in the study area.

Experiments show that the three species of Necrophorus will bury corpses at the same time of year. Necrophorus humator however, appears to be associated with large corpses and rarely buries the corpses exploited by the other two species. Corpse selection by Necrophorus has been noted before. Necrophorus germanicus is recorded as occurring mainly on large corpses and only accidentally on small ones (Reitter, 1909; Portevin, 1926a). A closely related species, Necrodes littoralis, is known as an inhabitant of large corpses (Birch, 1967; Birkett, 1969a, b, 1973; this study Table 3:5). Portevin (1926a) records N.humator as an inhabitant of medium corpses, while N.vespilloides, N.vospillo and N.investigator are found on small corpses. Springett (1967) suggests that Necrophorus humator and N.investigator may prefer small bird corpses to those of rabbits. Corpse selection may, therefore, occur in several species of burying beetle. Experimental data suggests that N.investigator may prefer rat sized corpses to those of mice. Supporting evidence from the field is, however, contradictory and suggests that in some circumstances

both N.investigator and N.vespilloides will bury both rats and mice. In any event, the rat sized corpses which N.investigator may prefer are unlikely to occur in the study area, the most numerous corpses probably being those of shrews, voles and small birds. Even these may be present in smaller number when N.investigator is breeding than earlier in the season. Therefore, even if corpse selection could be proved to occur experimentally, it is likely that N.vespilloides and N.investigator will be burying the same type of corpse in the study area.

N.humator is unlikely to compete with the other two species as it exploits a different resource. N.vespilloides and N.investigator occur in the same place, at the same time and bury the same type of corpse, and so there is a potential for interspecific competition when the breeding periods of the two species overlap. Evidence that interspecific competition actually occurs is more circumstantial. The appearance of N.investigator is correlated with the end of the breeding of N.vespilloides about a month later. Although mature N.vespilloides may be present after this time, they do not seem to breed. This suggests that when sufficient N.investigator emerge to bury all the available corpses, N.vespilloides stop breeding. There is no direct evidence however that N.vespilloides stops breeding because of competition, and other explanations are possible for the observations. For example, the factor which caused N.investigator to emerge late in 1974 could also have prolonged the breeding of N.vespilloides. Competition does occur under laboratory conditions, however, and N.investigator buries all corpses when in containers with N.vespilloides. In the field, N.vespilloides buries a smaller proportion of corpses in the presence of N.investigator than in its absence. N.investigator also buries fewer corpses when N.vespilloides is present than when it is absent. It is possible that

the reduction in the proportion of corpses buried may be due to competition between the species. If there is competition pressure on either or both of the species, it is perhaps surprising that displaced individuals do not use the 46% of corpses unburied, thereby increasing the overall proportion of corpses buried. This may not occur because most of the corpses not buried by Necrophorus are in fact unavailable to the beetles, being taken by scavengers or other insects. Whatever the reason, the proportion of corpses buried by both species together is the same as that buried by each species individually. Decreasing numbers of N.vespilloides at the end of its breeding season and increasing numbers at the beginning of that of N.investigator may have some effect on the relative proportion of corpses buried. In addition, the condition of the beetles in the N.vespilloides population may change towards the end of the breeding season. There will be more post reproductive and fewer mature individuals. The quality of mature N.vespilloides late in the breeding season may also change, as these individuals may have lived for some time without breeding. There is some evidence that N.vespilloides may bury fewer corpses at this time of year even when N.investigator is not present.

As far as the criteria for demonstrating competition are concerned, the evidence suggests that only (a) is convincingly demonstrated, i.e. the potential exists for interspecific competition between N.vespilloides and N.investigator. Some field and laboratory data may be interpreted as indicating that interspecific competition actually occurs, although other interpretations are possible. At present, therefore, the problem of whether interspecific competition occurs in the field must remain unsolved.

Competition can be demonstrated in the laboratory, and it is

of interest to speculate on the relationship between N.vespilloides and N.investigator if competition does occur in the field. The laboratory experiments indicate that N.investigator is the superior competitor, and buries all corpses in competition with N.vespilloides. Even allowing for a less clear cut pattern in the field, N.investigator seems to have the competitive edge. Field results on the termination of breeding by N.vespilloides on the appearance of N.investigator may confirm this. The question is then - why does N.investigator not come forward in time and oust the N.vespilloides population? Nothing seems to be preventing this from occurring. N.vespilloides seems unable to do so, and N.investigator on Inchcailloch is not tied to one type of corpse appearing at one time of year, as is the case with tern chicks on Inner Farne (Springett, 1967). Indeed, as far as individual N.investigator are concerned it seems advantageous to emerge earlier. Not only is the vulnerable soil-dwelling stage shortened, but more carrion may be available earlier in the season. That N.investigator can emerge earlier in the year is shown by the individuals recorded at the Ross Point in May. Therefore, are the populations of the two species static, or in a state of dynamic change? Some evidence that burying beetle populations can change comes from a consideration of species lists. N.vespillo was recorded from the Loch Lomond area in the past (Elliot, Laurie and Murdoch, 1901) but was not found during the present study. Similarly, N.vespillo was recorded in Monks Wood, Huntingdon before 1926 but is now believed to be extinct, although N.vespilloides, N.humator and N.investigator are still present (Welch, 1973). N.vespilloides has similar habits and life cycle to N.vespillo and it is tempting to suggest that the disappearance of N.vespillo may have been due to competition with N.vespilloides. In the absence of more data, this must remain speculation. Only by removing each species from an area and observing

the effect on the breeding of the other species will the occurrence of competition and its effects on the population be effectively demonstrated. This could be done relatively easily on Loch Lomond, where adjacent islands with similar Necrophorus populations could be treated differently.

Although not examined during this study, there is a second period when competition may occur between N.vespilloides and N.investigator. This is at the end of the season when the former is searching for carrion to feed on prior to diapause and the latter is still seeking corpses for breeding. Burial of a corpse by N.investigator means that it becomes unavailable to N.vespilloides as food. The more N.investigator successfully breeding, the less able will N.vespilloides be to lay down fat reserves and so survive the winter. Competition at this time may have as important effect on the size of the breeding population in the following year as that occurring earlier in the season. Therefore the existence of competition during this period must be verified and its effects on the population assessed.

SECTION 4.

RELATIONS WITH RESOURCES

4. RELATIONS WITH RESOURCES

4.1. Introduction

Two main resources are used by adult burying beetles, namely: a corpse for breeding and food. Although confused in the past, they should be regarded as separate resources. Burying beetles have other requirements, such as a place to overwinter but these were not examined in this study.

a) A corpse for breeding

Everyone who has examined the breeding of Necrophorus (Pukowski, 1933; Roussel, 1964a, b; Springett, 1967) has recorded individual variation in, for example, clutch size or survival of the larvae, but no-one has attempted to explain this. In this study, several aspects of reproduction were examined and compared with other variables to assess and explain variations between individuals. Some of the aspects of reproduction examined were - number and size of eggs, number and size of larvae, survival of larvae during development and use of food by larvae.

b) Food.

The food of burying beetles has received little attention, as it has been generally accepted that burying beetles feed mainly on carrion. Some observations suggest, however, that Necrophorus exploit food sources other than carrion (Pukowski, 1933; Elton, 1966; Springett, 1967). In this study, a laboratory investigation was carried out on the use of food other than carrion by Necrophorus and its effect on the growth and survival of individual beetles. Particular attention was paid to the period prior to breeding where food is required to mature the gonads, as well as for survival, and the period prior to diapause, when food is required to build up fat reserves for the winter.

4.2 Materials and Methods

4.2.1 Field Experiments

4.2.1.1. Experimental Procedure

The study area, type of corpse used and general experimental procedure were as described previously (3.2.), with the following additions. A few corpses were dug up at regular intervals. The species of beetle burying the corpse was recorded and the progress of breeding monitored. If required for further examination, the corpse was reburied. When an experiment was terminated, the corpse was dug up, transferred with larvae to a 1 lb Kilner jar and taken to the laboratory. Adults, if present, were carried in separate Kilner jars. If the larvae were to be allowed to pupate, the corpse was put into a flowerpot, 13cms in diameter and 12cms high, along with the surrounding soil. To prevent emergent insects escaping, a perspex cover, 20cms high topped with gauze was placed over the flowerpot and the holes in the bottom of the pot were sealed with adhesive tape. Fine holes were punched in the tape to allow drainage of water. The flowerpot was then kept in an insectary until adults emerged.

Larvae and pupae were removed from the corpse for weighing using fine forceps (first and second instar larvae and pupae) or by hand (third instar larvae). The live weight of larvae and pupae was recorded, after all soil particles had been removed with a camel hair brush.

Experimental alteration of clutch size.

In some experiments, the clutch size of burying beetles was altered artificially. First instar larvae were transplanted,

due to the difficulty of finding eggs in the field. First instar larvae were removed from the corpse and counted. In an experimental corpse, the number of larvae was halved or doubled, the altered clutch replaced on the corpse and the nest reburied inside a flowerpot. The larvae from clutches halved in size were kept in a Kilner jar and used to make up the clutches which were doubled. Control corpses were treated in the same way but all the larvae were replaced. Nests were taken to the laboratory when larvae reached the late third instar. Dispersing pupae were weighed and then replaced in the flowerpot. In some cases, flowerpots were kept in an insectary for examination of pupae and newly hatched adults. In others, pots were returned to the field and left there during the pupation period. As soon as newly emerged adults were detected, the pots were returned to the laboratory for examination. Unless otherwise stated, the mouse corpses used in transplant experiments weighed 25 ± 1gm.

4.2.1.2. Description of experiments

The aim of these experiments was to assess the relationship between burying beetles and a corpse in terms of mortality of the larvae. This involved recording the level of mortality in normal clutches and in abnormal clutches, altered by adding and subtracting larvae from normal clutches.

a). Mortality in normal clutches.

These experiments were designed to estimate larval mortality at each stage in development. Mice and rats were placed in the field on a grid, at intervals during 1974, and all data for the same species were combined for analysis. A total of 400 corpses were used in four replicates of 100 each.

To follow mortality, corpses were dug up at intervals, once a day in the early stages of development, once a week later, and the number of larvae counted. A reduction in the number present was assumed to be due to mortality. Individual corpses were followed as long as possible. Eggs were not easily found in the soil round a buried corpse, and repeated digging up of a corpse often resulted in females abandoning their eggs. Therefore no clutch was observed from egg to adult. The number of clutches that were observed in each stage of larval development is shown in table 4:12. For 62 N. vespilloides clutches and 31 of N. investigator, it was possible to follow larval mortality from first instar to pupae. This allowed a comparison between clutch size and mortality in normal clutches.

The species burying each corpse was noted and used in the experiments on competition.

b). Mortality in artificial clutches.

In these experiments, the effect of transplanting larvae from corpse to corpse, as described in 4.2.1.1., on larval mortality and its cause were explored.

In the main transplant experiment, mice weighing 25gms were used. 600 such mice were used in 1974 and 1975, in two replicates of 200 - in June (N. vespilloides only - and two of 100 in late August (N. investigator only). Of the corpses buried, 271 had the clutches of larvae on them halved or doubled in size - the experimental clutches - and 123 served as controls. Clutch size, mean weight at dispersal, mortality at dispersal and mortality on emergence were recorded from each clutch.

In a second transplant experiment, in June 1975, mice weighing 15, 10 and 5 gm mice were used, 60 mice of each size being put out. Only the number of callow adults emerging was recorded.

Results obtained in the transplant experiments were not used for any other experiment.

c). Number of larvae on abnormal corpses.

The number of larvae found on some abnormal corpses used in competition experiments were noted. This included clutches on 131 supermice and 131 light rats, buried during 1974.

4.2.2. Laboratory experiments

4.2.2.1. Experimental Procedure

In general, laboratory procedures were as described in 3.2. with the following additions.

a\ Relations with the corpse.

Breeding burying beetles.

The container used for breeding Necrophorus was a 2 lb Kilner jar, three quarter filled with John Innes potting compost No.1. Air holes were pierced in the metal lid of the jar. A pair of burying beetles were put into the container along with a mouse or chick corpse and burial was allowed to proceed without disturbance. The Kilner jar was kept under normal daylight conditions in an insectary, shaded from the sun. The male was removed from the container if seen in the soil surface during an experiment. Nests were disturbed only for routine weighing and monitoring. Eggs and larvae were replaced on the corpse after weighing. The wet weight of the corpse was recorded immediately before use. After the larvae had dispersed, the remains of the corpse were removed from the soil, washed thoroughly to remove any adhering soil particles, blotted dry and weighed.

To follow changes in size during development, and mortality at different stages of development, pairs of beetles were allowed to bury mouse corpses. In the field, corpses were dug up and put into a flowerpot when development was well advanced but prior to dispersal of the larvae. Flowerpots were kept in the field until mature adults emerged. The corpses were only disturbed to count the larvae. In the laboratory, containers were examined at frequent intervals after burial of the corpse. Shortly after being laid, eggs were removed, weighed and replaced next to the side of the jar to make observation easier. Eggs were examined at regular intervals until they hatched. After hatching, larvae were weighed at six hour intervals up to 2 days from hatching, at 12 hour intervals up to five days from hatching and thereafter at two day intervals. All larvae in a clutch were weighed and the mean

live weight of the larvae in each clutch calculated. Moults were timed as accurately as possible, either by direct observation or by extrapolation between observations. To summarise growth rates, the weights of all larvae of the same age were combined to give a mean weight and standard deviation for each time interval. The results of several experiments were lumped and smooth curves fitted to growth curves by eye.

In experiments involving N.investigator prepupae, half of the containers were left out of doors overwinter and half in an unheated insectary. No differences were observed between the two treatments and results were combined for analysis.

Experimental alteration of clutch size.

In some experiments, the clutch size of burying beetles was altered artificially. Eggs, as far as possible of the same age, were removed from the soil and counted. In experimental containers the original clutch size was either halved or doubled, and the altered clutch replaced in the soil adjacent to the corpse. Eggs removed from halved clutches were kept in a blacked out petri dish until used to double the size of another clutch. In control containers, eggs were removed, counted and replaced. After treatment, corpses were reburied and the larvae were allowed to develop normally. On dispersal from the corpse, larvae were weighed then replaced in the Kilner jars. Adults were counted on emergence.

Dispersal of larvae.

To test how far larvae moved from the corpse during dispersal, an enclosure was built. Three large metal trays, 150cm x 70cm, were inverted and placed together to form a continuous surface area of 150 x 210cm. Wooden planks were set around the side to act as walls, and the whole 'tank' filled with woodland soil to a depth of about 10cm. A corpse containing late third instar larvae was placed in the centre. After one week, the distance of each pupae from the corpse was measured.

Corpse temperature.

After burial of the corpse, and before egg hatch, mercury thermometers were introduced into the centre of the corpse and into the crypt. The earth was replaced round the thermometers which were clamped to avoid disturbance to the larvae. Thermometers were left in place throughout larval development. No increase in mortality was observed in corpses with thermometers in place. Thermometers were also placed in the soil, level with the crypt and in the air above the experimental container. To measure relative fluctuations in temperature, readings were taken from each thermometer at noon and midnight throughout the

course of the experiment. Temperatures were also recorded at random intervals to assess the relations between temperatures in air, soil, crypt and corpse. Experimental containers were kept in daylight conditions in an insectary but were kept out of direct sunlight.

b). Relations with food.

Starvation experiments.

To assess the effects of depriving adult burying beetles of food, beetles were kept in moist John Innes potting compost in Kilner jars, under normal light conditions. No food was given and beetles were weighed every day until death.

Feeding experiments.

A feeding chamber, consisting of a crystallising dish with gauze cover, was used to test the readiness of burying beetles to take food other than carrion. Dry filter paper was glued to the floor of the chamber, which was left bare to prevent occupants of the chamber hiding from each other. Beetles to be tested were weighed and left in the chamber for one hour before the experiment began, to equilibrate. The food animal was weighed and put into the chamber; the experiment was then left under normal light conditions for 24 hours. At the end of this time, the burying beetle and the remains of the other animal were weighed. Animals used as food were: mealworms (Tenebrio molitor L. larvae), earthworms (Lumbricus spp.) of varying sizes, dead or alive adult Necrophorus, live Geotrupes, blowfly larvae, lycosid spiders, adult carabid and staphylinid beetles. When available, three species of oak defoliating caterpillars, larval and pupal Necrophorus were also used.

Weight changes of burying beetles fed on mealworms were examined to test the effects of feeding on other animals. In one

experiment, beetles were allowed to feed once a week. Beetles were weighed before feeding, given a weighed amount of mealworms and allowed to feed. If all mealworms were eaten more were added so that the beetle could feed to repletion. After 24 hours, the beetle and mealworm remains were removed from the feeding chamber and weighed. This was repeated once a week for the duration of the experiment. In a parallel experiment, beetles were weighed at weekly intervals, but were kept constantly supplied with an excess of mealworms, so that the beetles could eat when they required. In both these experiments, a group of beetles were kept in similar conditions and were weighed at the same time as the experimental animals but were not fed. Unless otherwise stated, beetles were kept in incubators at 15°C between feeds and during experiments.

Prediapause feeding.

To assess the relationship between prediapause feeding and adult survival overwinter, carrion was used as a food source. Immature adult N.vespilloides and a corpse were put into a plastic tray, two thirds filled with soil and leaf litter and covered with gauze. The holes in the bottom of the tray were left open to let water drain out. The tray was left outside at the University field station. The gauze was examined regularly for breaks. The number of beetles to become active the following spring was counted. 25 mice of similar weight were used as food, confidence intervals of their mean weights being 22.188 ± 0.824 gms.

4.2.2.2 Description of experiments

a). Relations with the corpse.

The aim of these experiments was to determine the relationship between burying beetles and the corpse, in the relatively constant conditions of a laboratory. In particular the number of eggs laid, the duration of development of the larvae and larval mortality were determined. Details of the number of corpses buried by each species were also used in the competition experiments.

1). Clutch size and the development of the larvae.

Clutches were examined at intervals, and the development of the larvae followed. 500 corpses, mainly mice, were used in two replicates of 100 in May / June 1974, two of 100 in August / September 1974, and one of 100 in June 1975. Results of replicates were combined for analysis. In each experiment the rate of development and variation in larval size between corpses were recorded. Where possible, the number of eggs and their size were also recorded. Relevant results on the effects of clutch size on mortality were also used.

2). Clutch mortality.

The level of mortality in normal clutches, and in those altered by the addition and subtraction of larvae was noted.

Normal clutches :

The aim of these experiments was to find out when and how mortality occurred during development of the larvae. 350 mice were used in these experiments, 250 in May / June 1974, and 100 in August 1974. In each replicate, the mice were divided into two groups, 150 of the first and 50 of the second replicates were used to determine mortality, and life tables were constructed from the results so obtained. The remaining corpses from each replicate were used to determine the

mortality from egg to emergence, and mean larval weight at dispersal. These served as a check on the effect of disturbance associated with counting larvae on mortality. As mortality did not differ between the replicates, the results combined to increase the numbers for analysis on the relation between clutch size, mortality and mean larval weight at dispersal.

Artificial clutches :

The technique used in this experiment is as described in 4.2.2.1. 450 mice were used in three replicates of 150, in May / June 1974 and 1975, and August 1974. Of those buried, 220 clutches were halved or doubled in size, and 101 were left unaltered as controls. For each corpse, clutch size, mean larval weight at dispersal mortality prior to dispersal and mortality experienced between dispersal and emergence were recorded. The species burying each corpse was noted and used for comparative purposes in the competition experiments.

A similar experiment was carried out on the clutches of larvae on six rats.

3). Corpse temperature.

Only one experiment was done, in May / June 1975, involving 60 mice, buried by N. vespilloides.

b). Relation with Food.

These experiments were designed to determine whether burying beetles will eat invertebrates, and whether this would prolong survival and even lead to weight changes. Beetles were either starved to determine length of survival without food,or fed invertebrates, and the length of time for which they survived noted. Beetles of unknown age, fed twenty four hours before the experiment, callow adults and overwintered adults (N. vespilloides only) were used in the experiments. Beetles

of unknown age were the most abundant and readily available.

1). Survival without food.

This experiment was carried out in June and again in August 1974. 53 N. vespilloides and 48 of N. investigator of unknown age were used. In addition, callow adults and freshly emergent adults were used whenever available. 62 callow and 25 freshly emerged overwintered adult N. vespilloides and 18 callow N. investigator were so used. The N. vespilloides adults of unknown age were weighed at regular intervals throughout the experiment.

2). Survival and weight changes on invertebrates.

100 adult N. vespilloides fed twenty four hours previously were used in a single experiment in June 1975. In addition, 50 freshly emerged overwintered adults collected from experiments in May and June 1975 were used whenever they were found. Half the beetles in each group was fed to repletion once a week, and the other half supplied with surplus food daily. Similar starved beetles were used as controls.

As a preliminary to these experiments, 98 N. vespilloides and 53 N. investigator of unknown age and freshly emerged were kept in a container with a conspecific. Inevitably one of the beetles was eaten by the other. The survivor was kept unfed to determine how long they survived. This was done whenever beetles became available, during 1974.

4.3. Results

4.3.1. Relations between breeding ecology and the corpse

4.3.1.1. Clutch size.

The number of eggs laid by the three species in the study area was measured and the length and weight recorded.

(1) Relationships between egg length and weight

No N.humator eggs were available for measurement, but the length and weight of 201 N.vespilloides eggs (2.007 ± 0.164mm, 2.067 ± 0.471mg) and 150 N.investigator eggs (2.316 ± 0.279mm, 3.471 ± 0.393mg) were examined. N.vespilloides eggs varied in weight from 1.0 to 3.26mg and those of N.investigator from 2.29 to 4.29mg. These eggs are shorter than those of N.vespillo (mean length 2.958mm, Pukowski, 1933), but their weight is similar (mean weight c 2mg, Roussel, 1964a).

There is a significant correlation between length and weight of eggs in both N.vespilloides ($r = 0.425$, d.of f. 199, $p < 0.001$) and N.investigator ($r = 0.757$, d.of f. 148, $p < 0.001$) (fig. 4:1). Both length and weight can, therefore, be used to measure the size of eggs.

(11) Mean clutch size

The mean clutch size of N.vespilloides (12.79) is larger than that of N.investigator (7.89) (Table 4:1). The number of eggs laid by the two species is significantly different ($r = 7.20$, d.of f. 248, $p < 0.001$). Further, N.investigator lays significantly fewer eggs per gm of corpse material than does N.vespilloides (Table 4:2). The mean number of eggs laid by N.vespilloides on mice is not significantly different from that on rats (Table 4:1) while the mean clutch size of N.investigator on the two types of corpse is significantly different. For further analysis all N.vespilloides clutches will be considered together, regardless of type of corpse, and the clutches of N.investigator

Fig. 4:1

Relationship between length and weight of

Necrophorus eggs

Each dot in the mean weight for each measured

length. Standard deviation omitted.

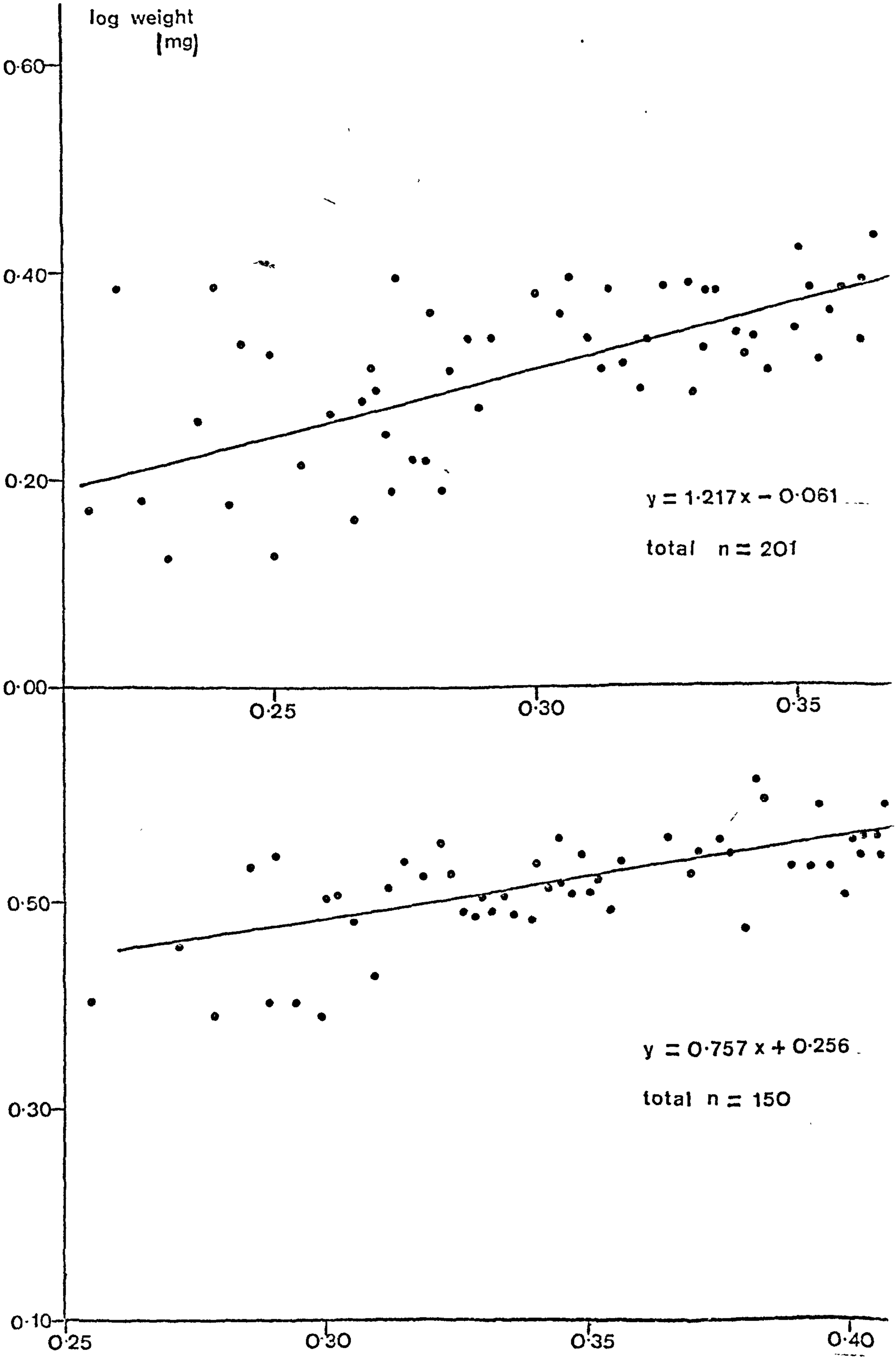

log weight
(mg)
0·60
0·40
0·20
0·00
0·25
0·30
0·35
y = 1·217x − 0·061
total n = 201
0·50
0·30
0·10
y = 0·757 x + 0·256
total n = 150
0·25
0·30
0·35
0·40
log length
(mm)

Table 4:1.

Mean number of eggs laid by Necrophorus

Type of Corpse	Number of eggs laid $\bar{x}$	SD	Number of females
N.vespilloides			
mice	12.87	6.05	138
rats	12.32	4.20	25
Total	12.79	5.8	163

Difference between number of eggs laid on mice and rats not significant ($t = 0.435$ doff 161 $p > 0.05$)

N.investigator			
mice	6.43	2.84	49
rats	9.76	3.42	38
Total	7.89	3.51	87

Difference between mean number of eggs laid on mice and rats significant ($t = 4.96$ doff 85 $p < 0.001$

Table 4:2.

Number of eggs laid by Necrophorus in relation to corpse weight

Species	Number of eggs laid per gm corpse weight					
	mice			rats		
	$\bar{x}$	SD	No. corpses	$\bar{x}$	SD	No. corpses
N.vespilloides	0.565	0.334	138	0.054	0.021	25
N.investigator	0.299	0.153	49	0.043	0.019	38
	$t = 5.371$ doff 185			$t = 2.156$ doff 61		
	$p < 0.001$			$p < 0.001$		

laid on different types of corpse will be considered separately.

The mean clutch size of N.vespilloides under experimental conditions (12.79 ± 5.8; Table 4:1), is not significantly different from the mean number of eggs in mature females (13.00 ± 6.566; Table 2:8) ($r = 0.11$, d.of f. 171, $p > 0.05$). This suggests that all the eggs matured by N.vespilloides are laid under experimental conditions. Similar comparison for N.investigator differ, depending on the type of corpse. The mean number of eggs in mature females (9.83 ± 4.35; Table 2:8) is not significantly different from the mean number of eggs laid on rats (9.76 ± 3.42; Table 4:1) ($r = 0.045$, d.of f. 42, $p > 0.05$) but is significantly different from that laid on mice (6.43 ± 2.84) ($r = 2.61$, d.of f. 53, $p < 0.05$). Therefore, when rats are buried by N.investigator under experimental conditions all the eggs matured are actually laid. Fewer eggs are laid on mouse corpses than are present in mature N.investigator females.

(111) Variation in clutch size.

The number of eggs laid by female burying beetles varied (fig. 4:2). Variation in clutch size was compared with mean egg weight, female body weight, male body weight and corpse weight. Eggs were not weighed individually; the total weight was recorded and the mean egg weight found by division. Mean egg weight was not significantly correlated with female body weight (N.vespilloides, $r = 0.093$, d.of.f 161, $p > 0.05$; N.investigator, $r = 0.162$, d.of f. 85, $p > 0.05$).

Mean clutch size was not correlated with egg weight, female body weight or male body weight (Table 4:3) or for N.vespilloides with corpse weight (fig. 4:3). There was a positive correlation between the mean clutch size of N.investigator and corpse weight (fig. 4:4). This relationship was not observed when mouse and rat corpses were considered

Fig. 4:2

Variation in clutch size of Necrophorus

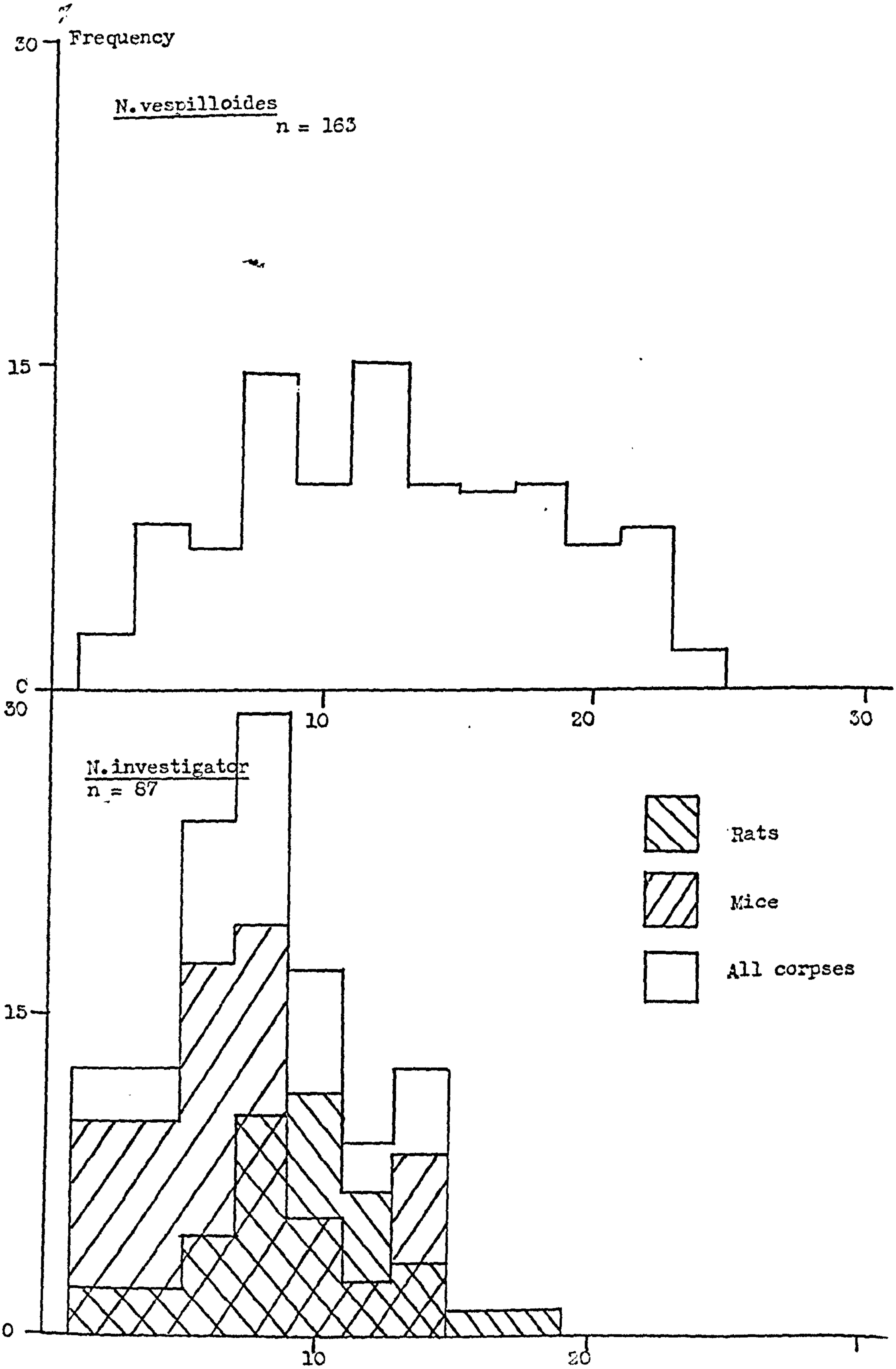

Frequency
N.vespilloides
n = 163
30
15
0
10
20
30
N.investigator
n = 87
15
0
10
20
Rats
Mice
All corpses
Number of eggs / clutch.

Table 4:3

Relation between mean clutch size and other variables

Variable	Correlation with mean clutch size					
	N.vespilloides			N.investigator		
	r	doff	p	r	doff	p
mean egg weight	0.031	161	>0.05	-0.015	85	>0.05
female body weight	0.044	161	>0.05	0.011	85	>0.05
male body weight	0.022	161	>0.05	0.144	85	>0.05
corpse weight(total)	0.085	161	>0.05	0.457	85	<0.001
Corpse weight (mice)	-	-	-	0.011	47	>0.05
Corpse weight (rats)	-	-	-	0.003	36	>0.05

Fig. 4:3

Relationship between corpse size and clutch size

of N.vespilloides

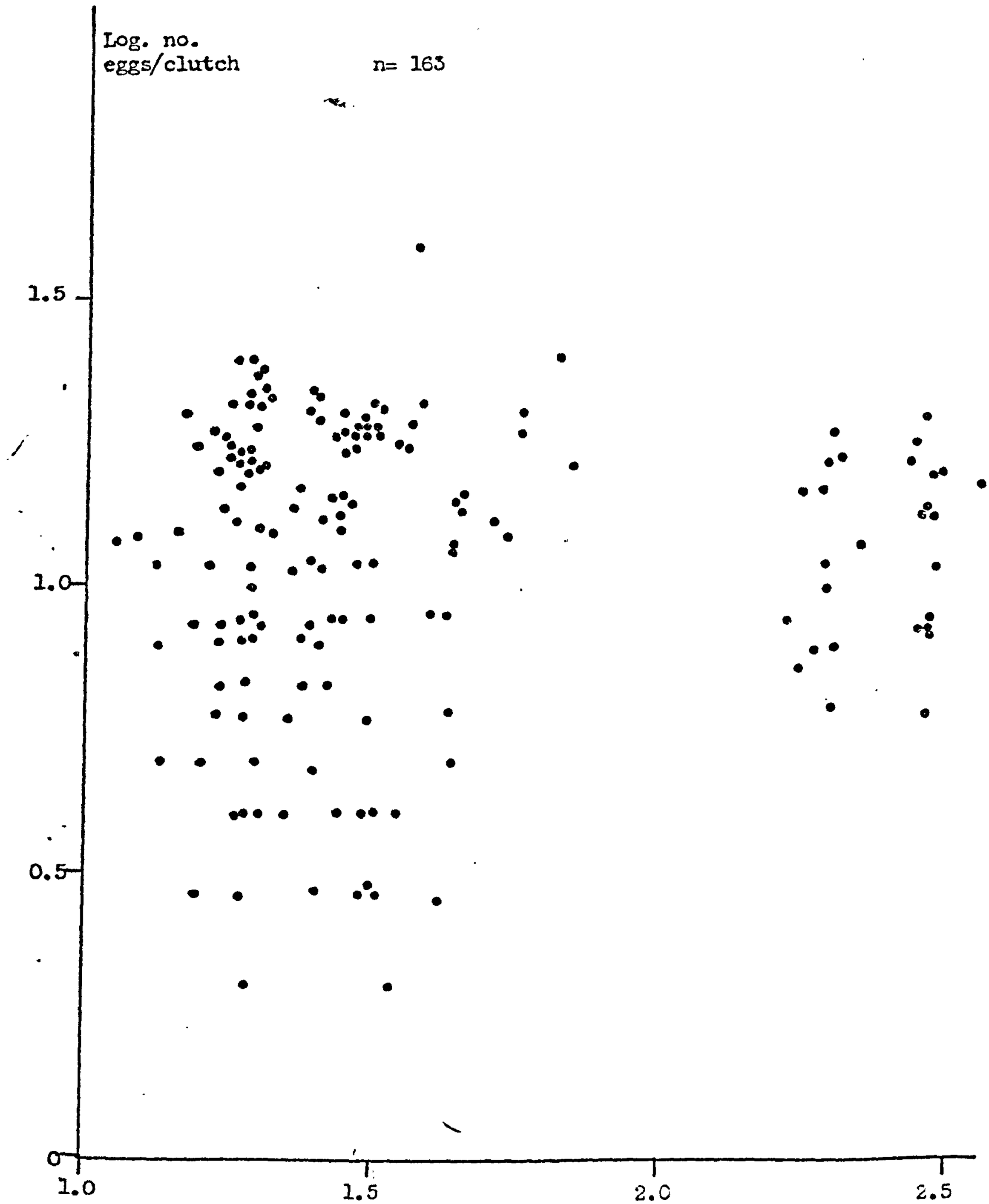
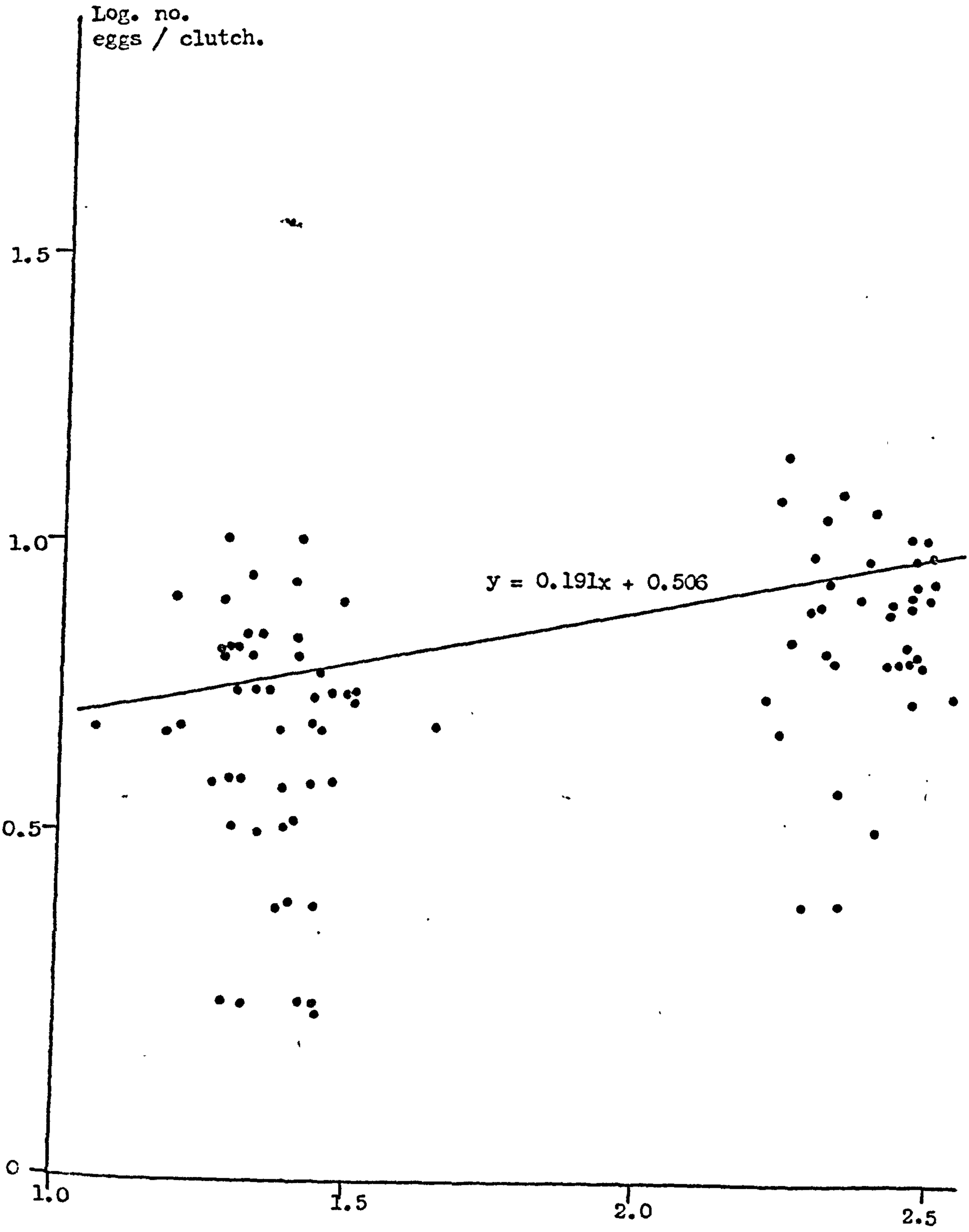

Log. no.
eggs/clutch
n= 163
1.5
1.0
0.5
0
1.0
1.5
2.0
2.5
Log10 corpse
weight

Fig. 4:4

Relationship between corpse size and clutch size of

N.investigator


Log. no.
eggs / clutch.
1.5
1.0
0.5
0
y = 0.191x + 0.506
1.0
1.5
2.0
2.5
Log. corpse
weight

separately (Table 4:3). One source of variation in the clutch size of N.investigator may therefore be related to the size of the corpse buried, fewer eggs being laid on mice than rats. Fewer eggs are laid on mouse corpses by N.investigator than are matured, while all mature eggs are laid on rats. The variation in egg number with corpse size may be due to female N.investigator not laying all the eggs they have matured on smaller corpses. The presence of eggs in post reproductive females (Table 2:8) shows that eggs are in fact retained by females after breeding.

Although this hypothesis may explain some of the observed variation, it is not the only explanation. Variation still occurs within each group of corpse sizes (figs. 4:3, 4:4). This major variation was not correlated with corpse size, the major variable at the time of egg laying. Consideration of Tables 4:1 and 2:8, moreover, shows that a similar degree of variation occurs in the number of eggs in mature females. This would suggest that variation may be caused before maturation of the eggs. The amount of food eaten by the female during development of the eggs may affect the number of eggs matured (Springett, 1967), but a detailed analysis of this was not carried out in this study.

4.3.1.2. Clutch development

(1) Development of the larvae

Observations on the changes in appearance and size of Necrophorus larvae during development have been made by Pukowski (1933) and Roussel (1964a) for N.vespillo, Roussel (1964b) for N.fossor (= N.interruptus) and Springett (1967) for N.investigator. In this study, information on weight changes of N.vespilloides and N.investigator is presented. No attempt is made to explain variations in rate of development between larvae or between clutches.

Seven stages in the development of Necrophorus are recognised

in the study, namely:

Egg stage - laying of egg to beginning of egg hatch;

first instar - end of egg hatch to beginning of first moult;

second instar - end of first moult to beginning of second moult;

third instar (larvae) - end of second moult to peak weight attained by larva;

third instar (prepupa) - peak weight to beginning of third moult pupation;

pupa - end of third moult to beginning of fourth moult (metamorphosis);

callow adult - end of fourth moult until cuticle is completely hardened.

The larval and pupal instars (fig. 1:2) are terminated by moults, but the prepupal stage is less easily defined. It is not itself an instar, but is part of the third instar, occurring somewhere between the second moult and pupation. The reasoning behind the definition adopted here is set out in Appendix 4.

The development of N.vespilloides and N.investigator is broadly similar, despite differences in life cycle. N.vespilloides took about 36 days to develop from egg hatch to emergence of callow adult (fig. 4:5) and N.investigator took about 28 days, although prepupae spent about 9 months in diapause (fig. 4:6). During the first instar, the larvae of both species increased in weight to about 10mg (Table 4:4). In the second instar, N.vespilloides increased to about 80mg in weight and N.investigator larvae to about 125mg. The maximum weight attained by N.vespilloides in the third instar was 310mg and by N.investigator 575mg. These weights were attained by day 5 and day 7 respectively. In the period between the onset of the prepupal stage and dispersal from the

Fig. 4:5

Development of N.vespilloides

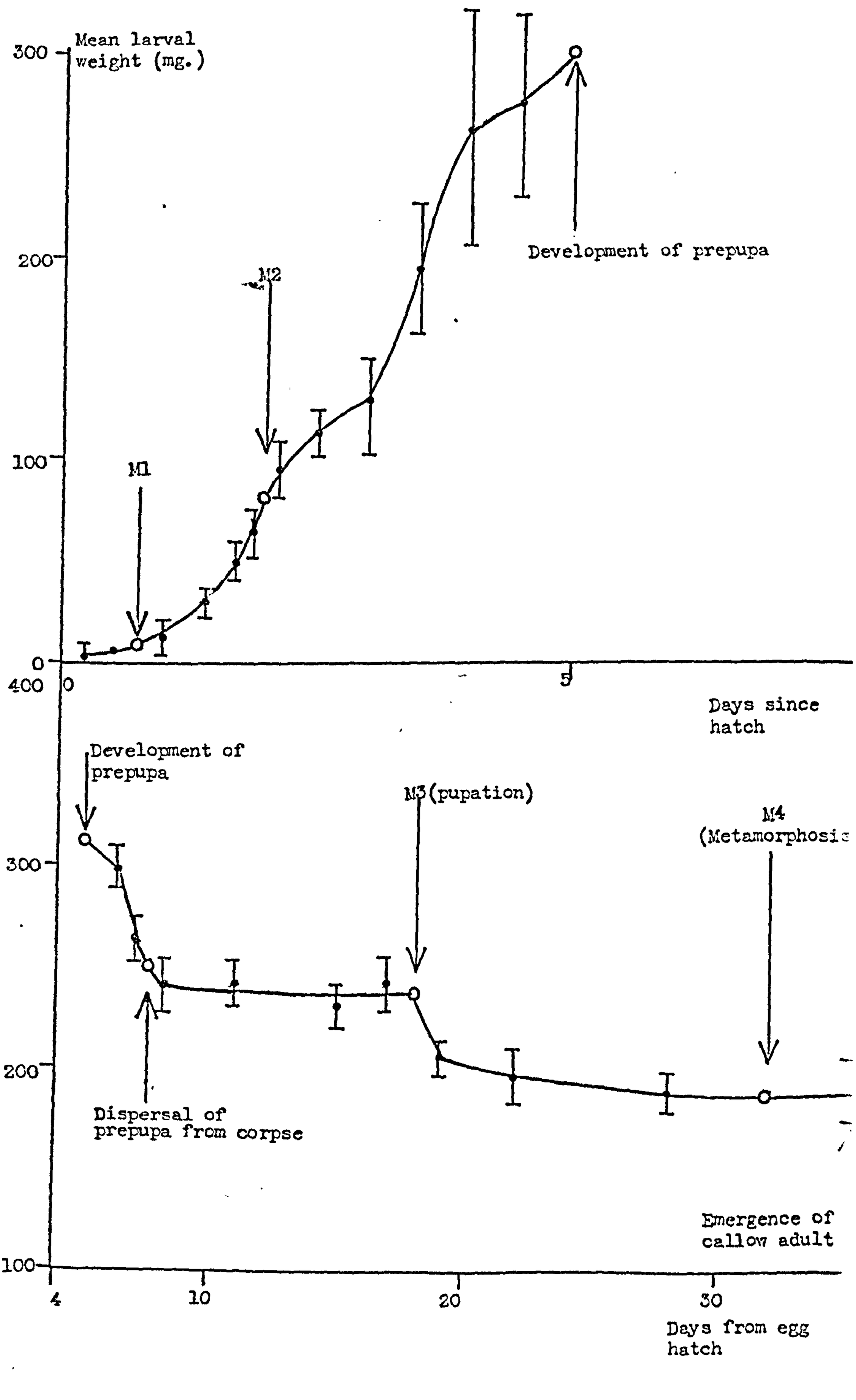

Mean larval weight (mg.)
300
200
100
0
400
300
200
100
M1
M2
Development of prepupa
0
5
Days since hatch
Development of prepupa
M3(pupation)
M4
(Metamorphosis
Dispersal of prepupa from corpse
Emergence of callow adult
4
10
20
30
Days from egg hatch

Fig. 4:6

Development of N.investigator

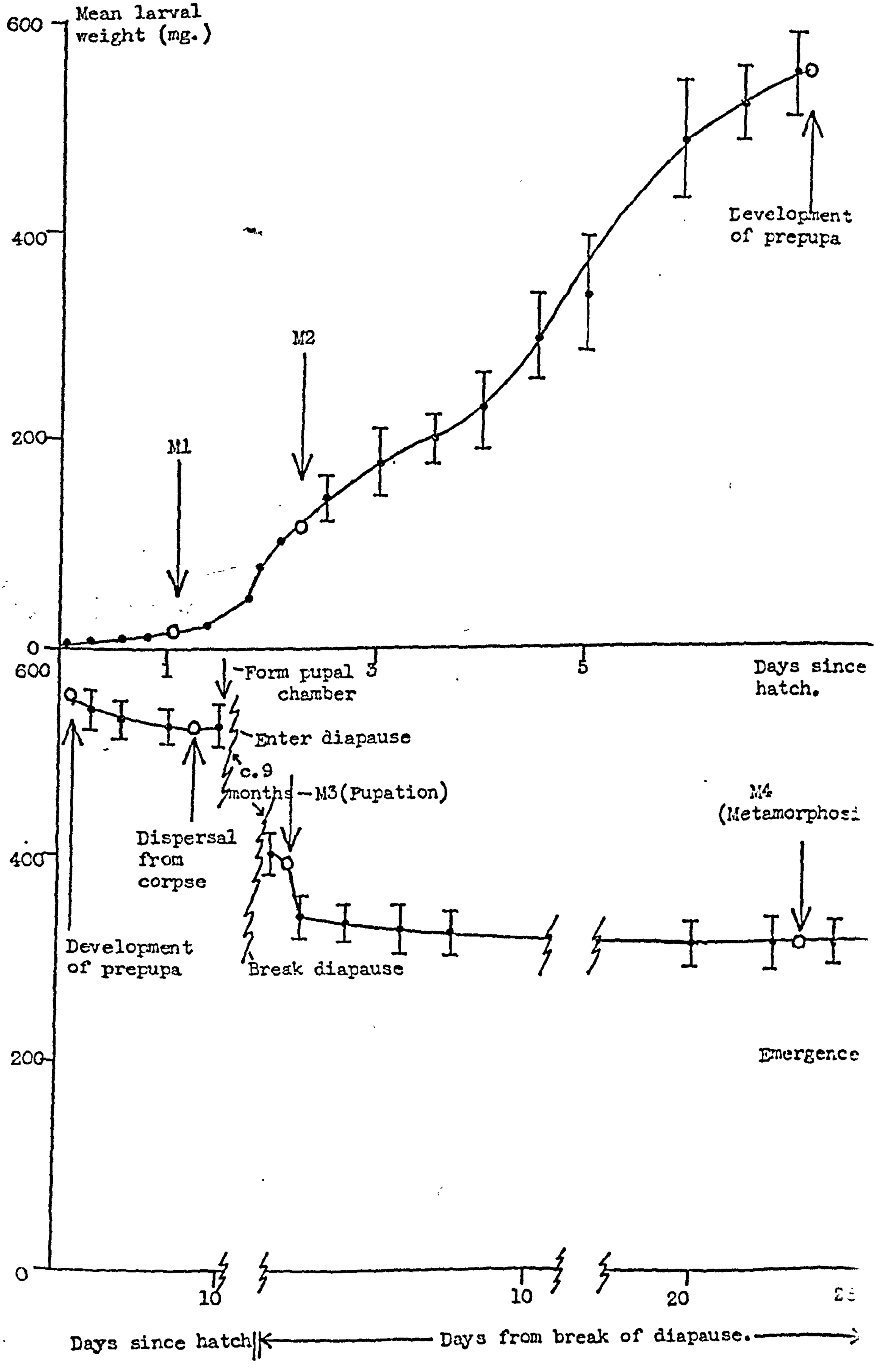

Mean larval weight (mg.)
600
400
200
0
M1
M2
Development of prepupa
Dispersal from corpse
Form pupal chamber
Enter diapause
c.9 months
M3(Pupation)
Break diapause
M4 (Metamorphosi
Emergence
1
3
5
Days since hatch.
10
10
20
Days since hatch
Days from break of diapause.

Table 4:4

Weight changes during each stage of *Necrophorus* development

Stage	Mean wt at beginning (mg)	Mean wt at end (mg)	wt change (mg)	Length of stage (hrs)	Mean wt change (mg/hr)
N.vespilloides					
I	2.0	9.31	+ 7.31	18.6	+0.39
II	9.31	77.28	+ 67.97	29.24	+2.32
III larva	77.28	310.11	+232.83	74.56	+3.12
IIIprepupa	310.11	239.81	- 70.20	310.32	-0.226
pupa	239.81	185.39	- 54.42	234.8	-0.163
Callow adult	185.39	187.39	+ 2.0	87.84	+0.023
N.investigator					
I	3.41	10.11	+ 6.70	25.5	+0.263
II	10.11	124.23	+114.12	26.5	+4.306
III larva	124.23	576.81	+452.28	123.2	+3.671
IIIprepupa	576.81	397.43	-179.38	(c.6,500)	(-0.028)
pupa	397.43	317.03	- 80.40	576	-0.140
adult	317.03	311.45	- 5.58	96.0	-0.058

corpse, N.vespilloides larvae lost about 60mg in 2 days, while N.investigator larvae lost about 25mg over three days. Overall N.vespilloides lost about 70mg during the prepupal stage, prepupation occurring at day 18. The total weight lost by N.investigator during the prepupal stage was about 180gms, associated with the prepupa spending the winter in diapause. It is not known when diapause starts and ends, but the mean period between formation of pupal chamber and pupation was 9.21 ± 1.236 months. In both species, pupation is associated with a weight loss, c. 40mg in N.vespilloides and c. 50mg in N.investigator. Pupation lasted about 14 days in N.vespilloides and 24 days in N.investigator, and after the initial drop, weight losses during pupation were low for both species. Adults emerged four days after metamorphosis.

There are slight differences in rate of development, N.vespilloides growing more rapidly than N.investigator during the first instar, and more slowly in the second. Growth is similar in the third instar, N.investigator reaching a higher weight than N.vespilloides, by having a longer period of growth (Table 4:4). Changes after development of the prepupae are similar for the two species, despite the differences in life cycle. This is presumably because physiological activity in the diapausing larvae of N.investigator is low. Differences in weight at maturity between the species reflect differences in egg weight, the ratio of egg weight to adult weight being similar in the two species ($\chi^2 = 0.001$, d. of f. 1, $p > 0.05$).

The observations on rate of development made during this study are, in general, similar to those made for N.vespillo (Pukowski, 1933; Roussel, 1964a) and N.fossor (= N.interruptus)(Roussel, 1964b). The data also resemble those of Springett (1967) for N.investigator, but his growth curves show peak weight occurring when larvae leave the corpse.

This disagrees with the observations of Roussel (1964a, b) and the results of the present study.

(11) Variation in larval size.

Variation in the size of individual larvae of the same clutch and between larvae of different clutches was observed. This was also noted by Roussel (1964a, b).

It is difficult to find a standard measurement of 'larval size'. Mean length and weights of each instar (Table 4:5) could be used, but the rapid changes in size during development reduce the value of mean figures for any instar, particularly the third. Differences in rates of development would also complicate the use of mean sizes of any instar to compare different clutches. The value used to characterise larval size was weight of larvae at dispersal from the corpse. It has been shown that larval weight does not change very much from dispersal to pupation (c.f. fig. 4:5) and so weight at dispersal is a good estimate of the ultimate size attained by the larvae. This is also recognisable as a standard stage regardless of the rate of preceding development. To test the value of mean larval weight at dispersal as a summary of the weight of larvae during development, this value was correlated with larval weights recorded during each preceding instar. As far as possible, all larvae were weighed at the same age, but no attempt was made to standardise different rates of development. Mean larval weight at dispersal was not correlated with first or second instar weight, but was correlated with third instar weight (Table 4:6), and is therefore a good indication of third instar weight. As most growth occurs during third instar, this is the most significant stage as far as variation in size is concerned.

The range of variation of mean larval weight at dispersal (MLWD) is shown in fig. 4:7. MLWD of different clutches ranges from

Table 4:5

Average weights of each stage of Necrophorus development.

Instar	Number	Length (mm) $\bar{x}$	Length (mm) SD	Weight (mg) $\bar{x}$	Weight (mg) SD
N.vespilloides					
Egg	201	2.007	0.164	2.067	0.471
I	128	4.988	3.380	4.429	1.958
II	140	8.544	3.380	28.073	2.856
III	631	17.40	0.713	198.80	15.046
pupa	248	14.33	2.422	237.43	46.14
Callow ♂	68	15.31	2.089	184.03	60.04
Callow ♀	78	15.60	1.889	185.51	58.50
adult ♂	84	15.44	1.865	186.81	52.11
adult ♀	90	16.09	1.864	202.62	52.45
N.investigator					
Egg	150	2.316	0.279	3.471	0.393
I	98	5.109	1.684	8.943	3.242
II	150	15.20	1.643	118.00	71.19
III	210	20.95	5.152	374.28	11.07
pupa	192	17.49	3.280	378.64	52.51
adult ♂	58	19.20	3.270	321.00	140.08
adult ♀	79	18.47	2.690	303.57	106.77

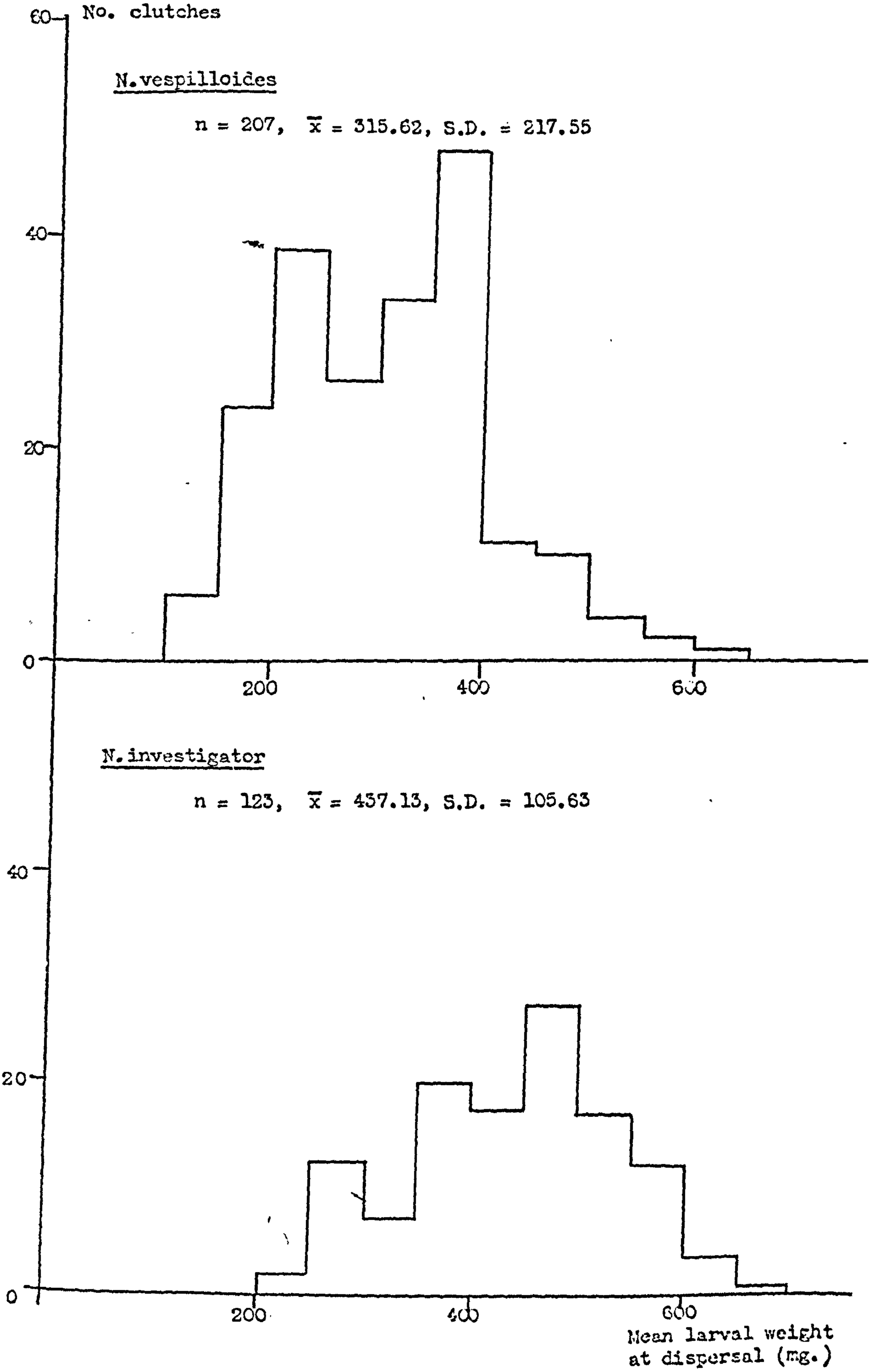
Table 4:6.

Comparison of Mean larval weight at dispersal with other variables.

	Correlation with MLWD					
	N.vespilloides			N.investigator		
Variable	r	doff	p	r	doff	p
first instar weight	-0.018	161	>0.05	-0.071	85	> 0.05
second instar weight	-0.038	161	> 0.05	-0.186	85	> 0.05
third instar weight	0.874	212	< 0.001	0.813	124	< 0.001
egg weight	0.112	161	> 0.05	0.119	85	> 0.05
female weight	0.092	212	> 0.05	0.013	124	> 0.05
number eggs laid	-0.054	161	> 0.05	0.101	85	> 0.05
corpse weight	-0.046	212	> 0.05	-0.028	124	> 0.05
No eggs/gm corpse material	0.110	161	> 0.05	-0.013	85	> 0.05

Fig. 4:7

Variation in mean larval weight at dispersal


No. clutches
N.vespilloides
n = 207, x̄ = 315.62, S.D. = 217.55
60
40
20
0
200
400
600
N.investigator
n = 123, x̄ = 437.13, S.D. = 105.63
40
20
0
200
400
600
Mean larval weight at dispersal (mg.)

100mg to 650mg for N.vespilloides and from 200mg to 700mg for N.investigator. These figures suggest that there is a considerable variation in weight of larvae between clutches. Variation in MLWD were compared with variations in female weight, egg weight and corpse weight (Table 4:6), and is not correlated with any variable at the early stages of development. This suggests that the variation exhibited at the end of feeding may originate during the third instar, possibly due to variation in the amount of food eaten by larvae.

A detailed analysis of variations in larval food consumption was not carried out. However, some preliminary data was obtained. The change in larval weight from egg hatch to dispersal was compared with the weight lost from the corpse in this period. These figures are only crude estimates of larval growth and food consumption respectively, as they take no account of losses in food to adults and micro-organisms, or larval defaecation and excretion. Adults, however, are believed to eat little while with the corpse (Pukowski, 1933; Springett, 1967) and microbial consumption of carrion may be insignificant compared with that of the insects themselves (Putman, 1977). The presence of antibiotic compounds in the crop contents of Necrophorus (Springett, 1967) may reduce microbial consumption still further. Even in sophisticated energy budget studies, such as that carried out by Putman (1977) the problem of mingling of larval food and waste products in this type of system cannot be overcome. This experiment was not considered detailed enough for this to be a major source of error. The total live (wet) weight of larvae produced from each corpse was calculated and divided by the wet weight lost by the corpse. The crude production figure so obtained is the total weight of larvae produced per mg corpse material.

Corpses buried by N.vespilloides lost 85.75% in weight between egg hatch and dispersal of larvae (n = 82). Putman (1977) shows that blowfly larvae consume over 80% of corpse material during development. No estimate of weight loss during development could be made for the 64 corpses eaten by N.investigator larvae, as only scattered pieces of bone were left when the larvae left the corpse. Therefore the amount of food consumed by earlier stages had to be calculated. Similar data were collected for N.vespilloides to assess how reliable this estimate of production was.

The weight of N.vespilloides larvae produced was similar when calculated at dispersal and earlier in development (Table 4:7), and so all the data were combined to give an estimate of 0.264mg larvae produced per mg food material. The corresponding figure for N.investigator was 0.266mg larvae per mg food. The means for the two species are not significantly different. These figures represent a gross conversion efficiency (i.e. growth/food consumed) of 26.43% for N.vespilloides and 22.62% for N.investigator. Although crude, they are of the same order of magnitude as the gross conversion efficiencies observed in both predacious and herbivorous insects (Calow, 1977; Humphreys, 1978; Wightman, 1978).

An estimate can be made of the number of larvae which corpses of a particular size could produce using the observed conversion rate. These figures can then be compared with the maximum number of larvae observed per corpse (Table 4:8). Assuming the whole corpse is eaten by N.investigator larvae, a production of 0.226mg larvae/mg corpse eaten and a mean weight at dispersal of 525mg, 10.76 N.investigator larvae would be expected on a 25gm corpse. The observed maximum production on this corpse size is about 10 (Table 4:16). The estimate of larval production is similar to the observed production in corpses of 25gm, but

Table 4:7

Conversion of food to larval material

	Number of corpses	Mg larval material produced/mg corpse used	
		$\bar{x}$	SD
N.vespilloides			
at dispersal	82	0.268	0.098
at earlier stages (I, II and III)	21	0.257	0.112
	r = 0.446	doff 101	p > 0.05
N.vespilloides (all data)	103	0.264	0.131
N.investigator (early stages)	30	0.226	0.163
	r = 1.32	doff 141	p > 0.05

Table 4:8

Estimated larval production on corpses of different sizes (*Necrophorus vespilloides*).

Original corpse weight(mg)	Wt consumed by larvae (mg)	Wt larval material produced(mg)	Estimated No. larvae produced by this corpse	Observed maximum production (Table 4:20)
25,000	21437	5659	22.64	27.54
15,000	12862	3395	13.58	23.4
10,000	8575	2264	9.05	26.3
5,000	4287	1132	4.53	19.00
150,000	128,625	33957	135.83	>100

Assumption

- 85.75% of corpse material is consumed by larvae;
- larval production is 0.264mg/mg corpse material consumed;
- mean weight of larvae at dispersal is 250mg (fig. 4:5).

becomes more of an underestimate as corpses become smaller. More larvae are produced on smaller corpses than would be suggested by the estimates.

(111) Dispersal of prepupae from the corpse.

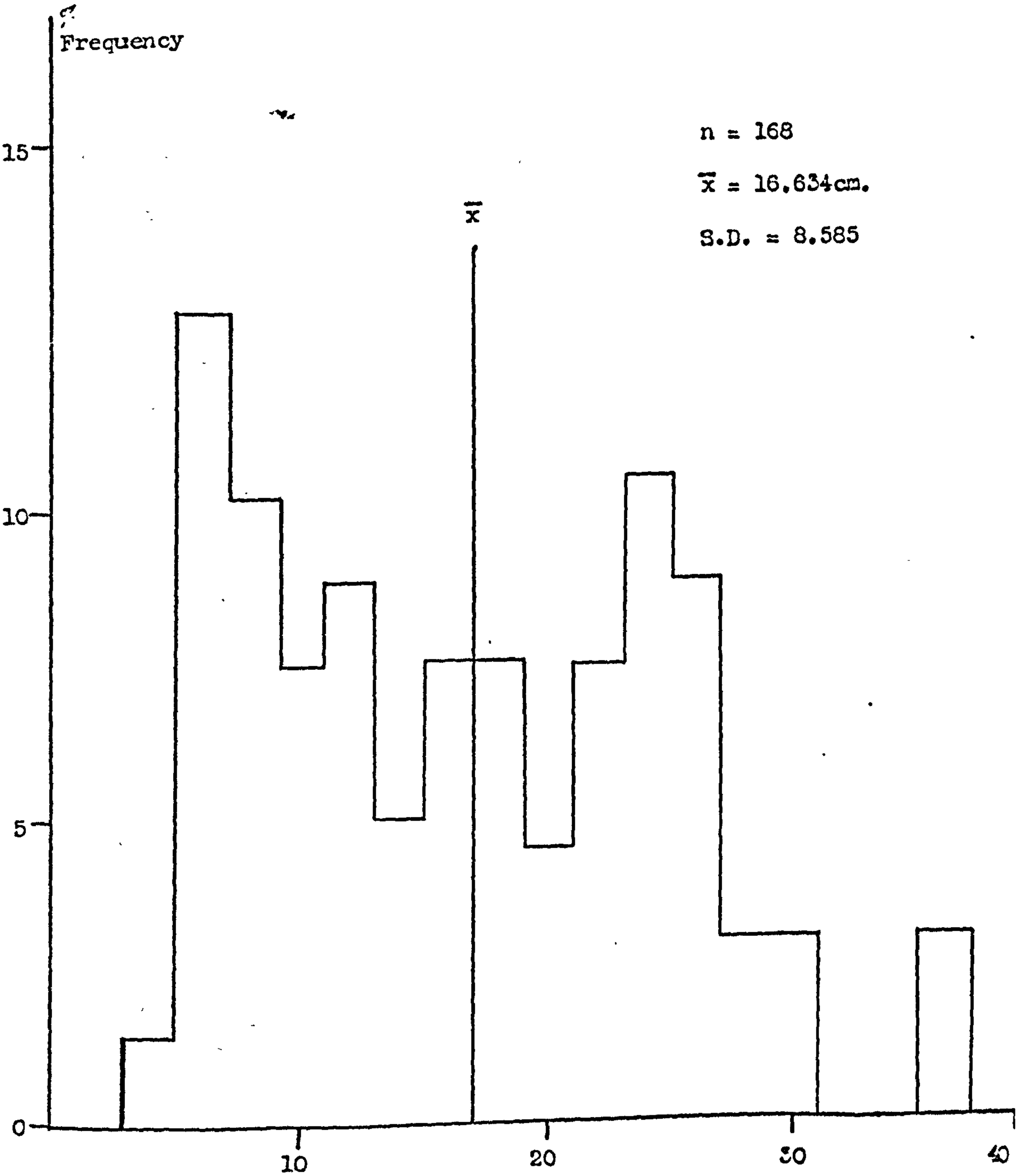
A simple experiment was carried out to assess how far prepupae wander from the corpse. The distance from the centre of the corpse to the pupal chamber was measured. There was no significant difference in the mean distance travelled by larvae from 8 mouse corpses ($\bar{x}$ = 17.70cm, s.d. = 8.723, n = 68), and from one rat corpse on which late third instar larvae from several different clutches were combined ($\bar{x}$ = 15.845cm s.d. = 6.263, n = 100) (t = 1.078, d. of f. 168, $p > 0.05$). All data were combined to give a mean distance from corpse to pupation chamber of 16.634cm, s.d. 8.585, n = 168 (fig. 4:8).

The shortest distance travelled was 4cm, the longest 42cm. Springett (1967) estimated that N.investigator travelled less than 5cm on dispersal. Some prepupae were observed crawling on or near the soil surface and through the leaf litter. These individuals took from 2 to 16 hours ($\bar{x}$ = 3.8hrs, n = 32) to reach the place where the pupal chamber was formed.

The mean distance from each pupa to its nearest neighbour in the combined clutch was 2.56cm, s.d. = 1.759, n = 100. This was compared to the distance to nearest neighbour in a randomly distributed population by the method of Clarke and Evans (1954). The method and results are summarised in Appendix 5. There is a significant difference between the observed and random distributions (d = 5.99, $p < 0.001$) and as the observed nearest neighbour distance is less than the distance expected, the population is held to be aggregated. This suggests that larvae pupate closer together than would be expected, possibly because they disperse from a central point. Even so, aggregation is less intense than would be the

Fig. 4:8

Distance travelled by prepupae during dispersal


f
Frequency
15
10
5
0
10
20
30
40
x̄
n = 168
x̄ = 16.634cm.
S.D. = 8.585
Dispersal distance. (cm.)

case if the prepupae did not disperse. Dispersal may reduce the probability of larvae being found by predation and so increase the chances of survival.

4.3.1.3. Clutch mortality.

Springett (1967) studied mortality of N.investigator and N.humator larvae and showed that the mortality of larger N.investigator clutches was higher than that of smaller clutches. In this study, corpses were examined at different stages of development to assess when mortality occurred, the level of mortality in normal clutches and to explain any variation that might be observed.

(1) Distribution of mortality in development.

The number of larvae present at the beginning of each instar was counted on 102 mouse corpses buried in the laboratory by N.vespilloides, and 50 mice buried by N.investigator. Larvae were counted as near as possible to each moult, and individuals disappearing between counts were assumed to have died. Results did not differ between replicates and so all results were combined for analysis. From the numbers dying at each stage, life tables were constructed for the development of Necrophorus, using the method of Birch (1948), Caughley and Birch (1971) (Tables 4:9, 4:10). Developmental mortality of N.vespilloides and N.investigator in the laboratory is compared in Table 4:11.

Mortality during development in the laboratory is low, 12.67% overall for N.vespilloides and 17.8% for N.investigator. This is less than that recorded by Springett (1967) who estimated the developmental mortality of N.investigator in the laboratory to be 24.54% and that of N.humator to be 25.6%. The main mortality was in the stages outwith the crypt, particularly in the pupal stage of N.vespilloides, and prepupae

Table 4:9

Developmental mortality of N.vespilloides:Life Table

(Laboratory)

Stage	Age (x)	Number larvae (fx)	l_x	d_x	q_x
Eggs laid	0	1327	1.00	0.028	0.028
eggs hatch	1	1290	0.972	0.007	0.007
moult 1	2	1281	0.965	0.005	0.005
moult 2	3	1274	0.960	0.006	0.006
dispersal	4	1266	0.954	0.013	0.014
moult 3	5	1249	0.941	0.064	0.068
moult 4	6	1164	0.877	0.004	0.005
emergence	7	1159	0.873		

Number of clutches = 102

$l_x = \frac{fx}{fo}$ = probability of surviving from birth to age x

$d_x = l_x - l_{x+1}$ = probability at birth of dying between age x and age x + 1.

$q_x = \frac{d_x}{l_x}$ = probability at age z of dying before age x + 1.

Table 4:10

Developmental mortality of N.investigator:Life Table

(Laboratory)

Stage	Age (x)	Number larvae (fx)	l_x	d_x	q_x
Eggs laid	0	337	1.00	0.021	0.021
eggs hatch	1	330	0.979	0.009	0.009
moult 1	2	327	0.970	0.003	0.003
moult 2	3	326	0.967	0.006	0.006
dispersal	4	324	0.961	0.089	0.093
moult 3	5	294	0.872	0.050	0.057
moult 4	6	277	0.822	0.000	0.000
emergence	7	277	0.822		

Number of clutches = 50

Table 4:11

Developmental mortality of Necrophorus in the laboratory:

Comparison of N.vespilloides and N.investigator

Stage of Development	N.vespilloides		N.investigator	
	% original number of eggs dying (dx)	% entering each instar dying (qx)	% original number of eggs dying (dx)	% entering each instar dying (qx)
Egg	2.788	(2.78)	2.077	(2.077)
I	0.678	(0.697)	0.890	(0.909)
II	0.527	(0.546)	0.297	(0.306)
III larvae	0.602	(0.628)	0.593	(0.613)
III prepupa	1.28	(1.34)	8.902	(9.259)
pupa	6.410	(6.80)	5.044	(5.782)
Callow adult	0.377	(0.429)	0.000	(0.000)
Total egg-emergence	12.66		17.80	

and pupal stage of N.investigator. Egg mortality was similar for the two species being about 2% in both. This is much less than that recorded by Springett (1967), namely 10% egg mortality for N.investigator in the laboratory and 14% for N.humator. For both N.vespilloides and N.investigator, mortality while within the corpse is less than 2%.

The overall mortality for N.investigator is higher than that of N.vespilloides because the prepupal mortality is higher. This difference is probably due to differences in the life cycles of the two species. The prepupa of N.investigator is the overwintering stage and so is longer in the soil than any other stage. It might be expected to run more risk of death. Mortality factors affecting burying beetles in the laboratory could be starvation, disease, failure to moult successfully and other intrinsic factors.

Using the observed mortality figures, and the mean number of eggs laid (Table 4:1), the number of adults produced from an average clutch in the laboratory can be estimated (Table 4:15). N.vespilloides lays more eggs than does N.investigator on mice and produces nearly twice as many adults. On rats, N.investigator produces nearly as many adults as does N.vespilloides on mice.

Estimation of mortality in the field is more difficult than in the laboratory. Eggs were not easily found in the soil round the corpse, and repeated digging up of the same corpse to count larvae often resulted in the female abandoning the clutch. In consequence, no clutch was followed through from egg to adults. The mortality at each stage in different corpses was recorded and the results combined to estimate the mortality throughout development (Table 4:12). Mortality of the instars within the corpse was not distinguished. Pupation, as usual in field experiments, took place in flowerpots. Pupal mortality in flowerpots

Table 4:12

Developmental mortality of *Necrophorus* in the field

Stage of development	*N.vespilloides*			*N.investigator*		
	Number clutches examined	Number at beginning of each stage	% mortality in each stage	Number clutches examined	Number at beginning of each stage	% mortality in each stage
Egg	12	148	4.73	6	43	4.65
larvae (within corpse)	57	741	2.16	39	229	1.75
prepupa	161	1834	5.62	53	269	23.42
pupa	257	3300	14.58	14	75	5.33
pre-emergence	84	1185	2.3	21	137	3.65

was compared with that from the dispersal experiment (4.3.1.2.) in which there was no limitation on the distance travelled by the larvae. There being no significant difference, the estimate of pupal mortality obtained in the field was considered reliable.

From the observed mortality, life tables were constructed for the development of a hypothetical population of 100 Necrophorus larvae (Table 4:13). The mortality of N.vespilloides and N.investigator at each stage is compared in Table 4:14. Mortality is highest in the pupal stage of N.vespilloides and prepupal stage of N.investigator. As in the laboratory, the overall mortality of N.investigator (34.56%) is higher than that of N.vespilloides (26.59%), because of higher prepupal mortality. More than half the developmental mortality of N.vespilloides and N.investigator occurs in the prepupal or pupal stages, the longest stage spent in the soil. Egg mortality, another soil stage, is similar in the two species at 4.7%. As in the laboratory, the stages in the corpse have low mortality, about 2% in both species.

Field and laboratory estimates of mortality incurred by larvae within the corpse are similar. The higher overall mortality in the field is due entirely to increased mortality in the soil-dwelling stages - egg, prepupa and pupa. In the field, predation and adverse weather conditions will affect larvae in the soil, in addition to the intrinsic factors causing death in the laboratory. Predation of pupae by Philonthus decorus Gr was observed in flowerpots in the field.

From the life tables (Table 4:13), the numbers of adults produced from an average burying beetle clutch in the field can be estimated (Table 4:15). Fewer adults are produced, of course, in the field than in the laboratory due to higher mortality. From an average clutch of about 13 eggs, N.vespilloides produces 9.4 adults in the field

Table 4:13

Life tables for the development of Necrophorus in the field, calculated from the observed mortality at each stage.

Stage	Age (x)	Number larvae (hypothetical) (fx)	lx	dx	qx
N.vespilloides					
eggs laid	0	100	1.00	0.047	0.047
eggs hatched	1	95.27	0.953	0.021	0.022
dispersal	2	93.21	0.932	0.052	0.056
moult 3	3	87.97	0.880	0.129	0.147
moult 4	4	75.14	0.751	0.017	0.022
emergence	5	73.41	0.734		
N.investigator					
eggs laid	0	100	1.00	0.047	0.047
eggs hatched	1	95.35	0.953	0.016	0.017
dispersal	2	93.68	0.937	0.220	0.235
moult 3	3	71.74	0.717	0.038	0.053
moult 4	4	67.92	0.679	0.025	0.037
emergence	5	65.44	0.654		

Table 4:14

Developmental mortality of Necrophorus in the field. Comparison of N.vespilloides and N.investigator

Stages of development	N.vespilloides		N.investigator	
	Estimated % of original number of eggs (dx)	Observed % entering each instar dying (qx)	Estimated % of original number of eggs (dx)	Observed % entering each instar dying (qx)
Egg	4.73	(4.73)	4.65	(4.65)
larval	2.06	(2.16)	1.67	(.175)
III prepupa	5.24	(5.62)	21.94	(23.42)
pupa	12.83	(14.58)	3.82	(5.33)
callow adult	1.73	(2.3)	2.48	(3.65)
Total egg emergence	26.59		34.56	

Table 4:15

Estimate of number of adults produced by an average *Necrophorus* clutch

Stage of development	Estimated number entering each stage					
	N.vespilloides (all corpses)		*N.investigator* mice		rats	
	Field	Lab.	Field	Lab	Field	Lab
mean number of eggs laid	12.79		6.43		9.76	
I	12.19	12.43	6.13	6.30	9.31	9.56
II	-	12.34	-	6.24	-	9.47
III larva	-	12.27	-	6.22	-	9.44
III prepupa	11.93	12.20	6.02	6.18	9.15	9.38
pupa	11.26	12.04	4.61	5.63	7.01	8.54
adult	9.62	11.26	4.36	5.35	6.64	8.11
emerged adult	9.40	11.22	4.20	5.35	6.40	8.11

and N.investigator produces 4.2 adults when mice are buries and 6.4 adults when rats are buried. Therefore, even when rats are buried by N.investigator, fewer adults are produced than result from the breeding of N.vespilloides.

(11) Variations in developmental mortality.

Laboratory experiments were carried out to examine variations in mortality, and the relationship between mortality and other variables. The survival to adulthood of larvae feeding on mice was recorded, together with egg number, and mean larval weight at dispersal. Larvae were only disturbed for weighing on dispersal from the corpse. The overall mortality from egg to emergence in this experiment was 13.3% for N.vespilloides and 16.95% for N.investigator. This is similar to the mortality observed previously (Table 4:11). Mortality varied from 0 to 50% with a noticeably skewed distribution in both species (fig. 4:9).

For comparison with egg number and mean larval weight at dispersal, mortality was expressed as log $\frac{n_1}{n_2}$, where n_1 = total number of eggs for all clutches of the same size and n_2 = total number of adults produced by all clutches of the same size. This is the k-value of Varley and Gradwell (1960).

In the laboratory, there is no correlation between mortality and mean larval weight at dispersal (N.vespilloides, $r = 0.106$, d.of f. 22, $p > 0.05$; N.investigator, $r = 0.334$, d.of f. 10, $p > 0.05$) or clutch size (N.vespilloides, $r = 0.285$, d.of f. 22, $p > 0.05$; N.investigator, $r = 0.291$, d.of f. 10, $p > 0.05$) (fig. 4:10). Similar results were observed in the field, where n_1 refers to first instar larval number rather than egg number. The relationship between number of first instar larvae and mortality in N.investigator is not significant

Fig. 4:9

Variation in developmental mortality

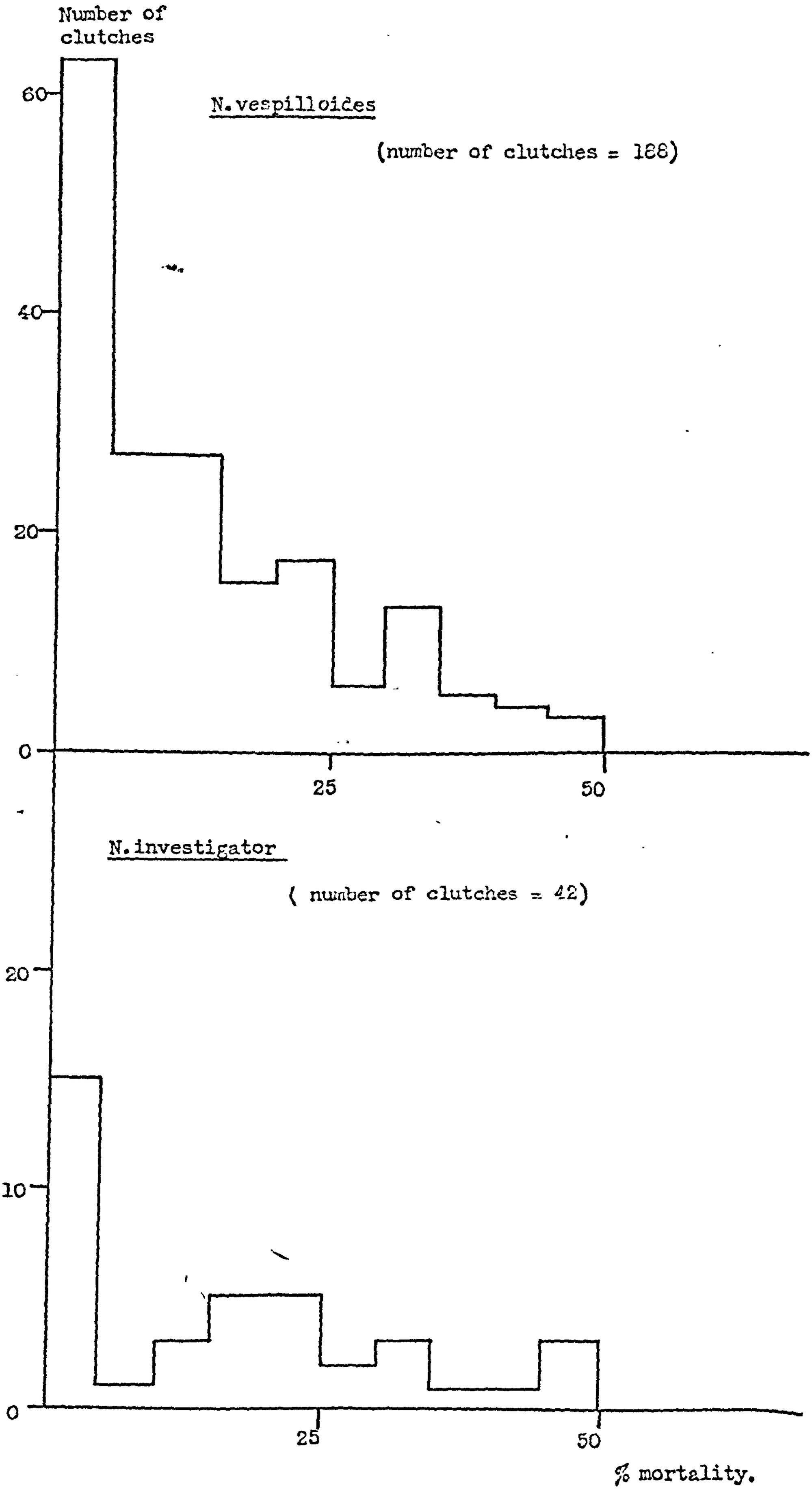

Number of clutches
60
40
20
0
25
50
N.vespilloides
(number of clutches = 188)
20
10
0
25
50
N.investigator
(number of clutches = 42)
% mortality.

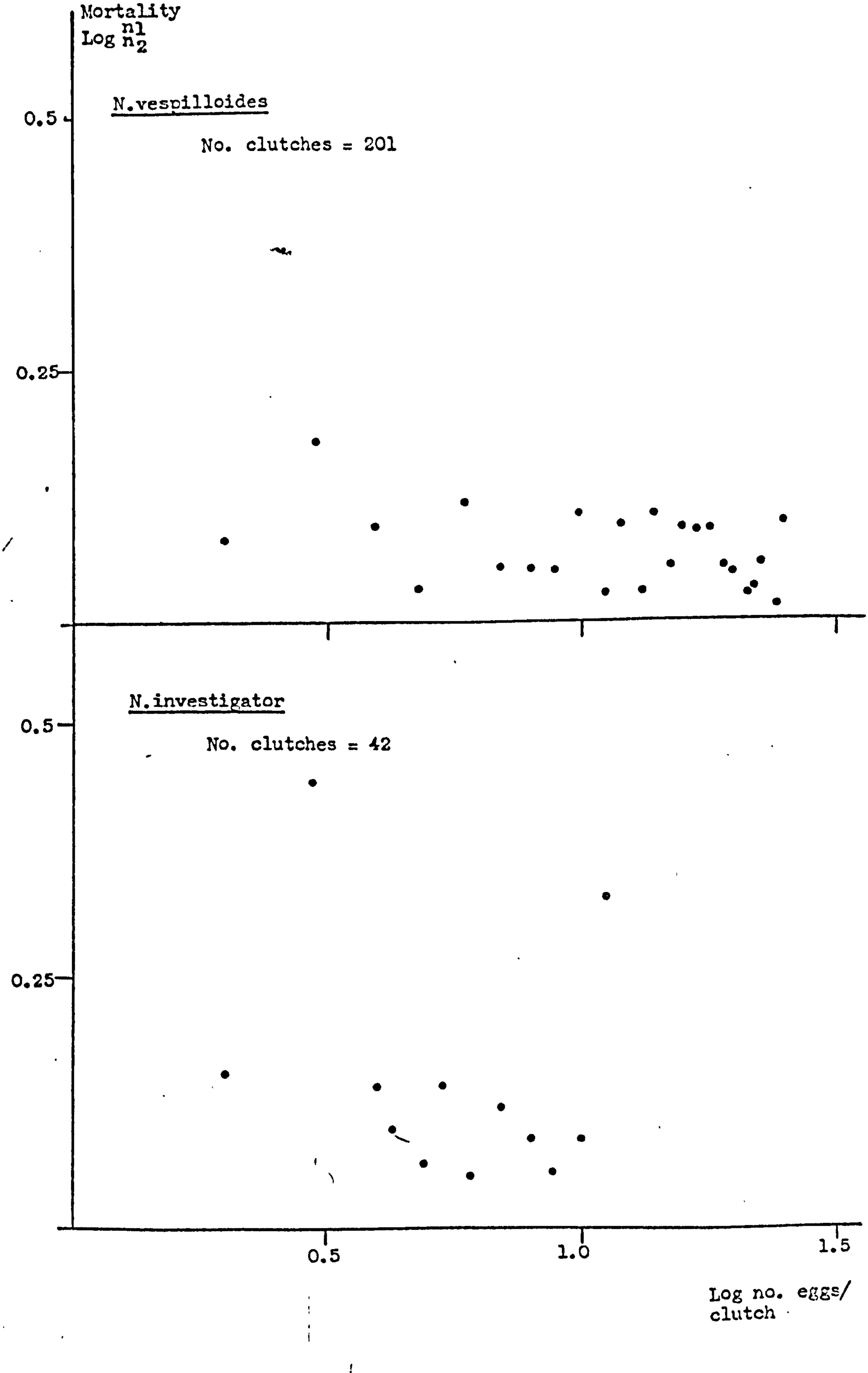
Fig. 4:10

Mortality during development (laboratory) :

Relationship between egg number and mortality

n_1 = total number of eggs

n_2 = total number of adults at emergence


Mortality
Log $\frac{n1}{n2}$
N.vespilloides
No. clutches = 201
0.5
0.25
N.investigator
No. clutches = 42
0.5
0.25
0.5
1.0
1.5
Log no. eggs/ clutch

($r = -0.305$, d.of f. 9, $p > 0.05$), but is significant for N.vespilloides ($r = -0.821$, d.of f. 15, $p < 0.001$) (fig. 4:11). The observed slope of the regression line for N.vespilloides is significantly different from $b = 0$ at $p = 0.05$, and the relationship appears to be inversely density dependent (Varley and Gradwell, 1968). This would indicate a synergistic effect between larvae. This correlation may be false, however, being an artefact of the low number of replicates in the smaller clutch sizes. Clutch size classes in the range 2 - 5 had only 1 - 2 replicates, as only 5 clutches were found in this range. A single larva dying in a small clutch with few replicates gives a high $\log \frac{n_1}{n_2}$ value, thereby distorting the relationship. If the four points representing 1 - 2 replicates are omitted, there is no correlation between clutch size and mortality of N.vespilloides in the field.

Both laboratory and field results suggest that mortality is low in normal clutches, and there is no relationship between developmental mortality and larval density or mean larval weight at dispersal. To explore more fully the relationship between mortality and other variables, the range of variation in clutch size was increased by transplanting larvae from corpse to corpse (Table 4:16). Although the range of variation has been effectively doubled, the mean clutch size is similar to that for control corpses. Eggs were transplanted in the laboratory and first instar larvae in the field. Clutch size, mean larval weight at dispersal, mortality at dispersal and mortality on emergence of adults was recorded for each clutch. Unless otherwise stated, the weight of mouse corpses used was 25gm $\pm$ 1gm, and that of rats 250gm $\pm$ 10gm. The results of transplant experiments carried out in 1974 and 1975 did not differ significantly and so all results were combined for analysis.

Fig. 4:11

Mortality during development (field) :

Relationship between clutch size and mortality

n_1 = total number of first instar

n_2 = total number of adults at emergence

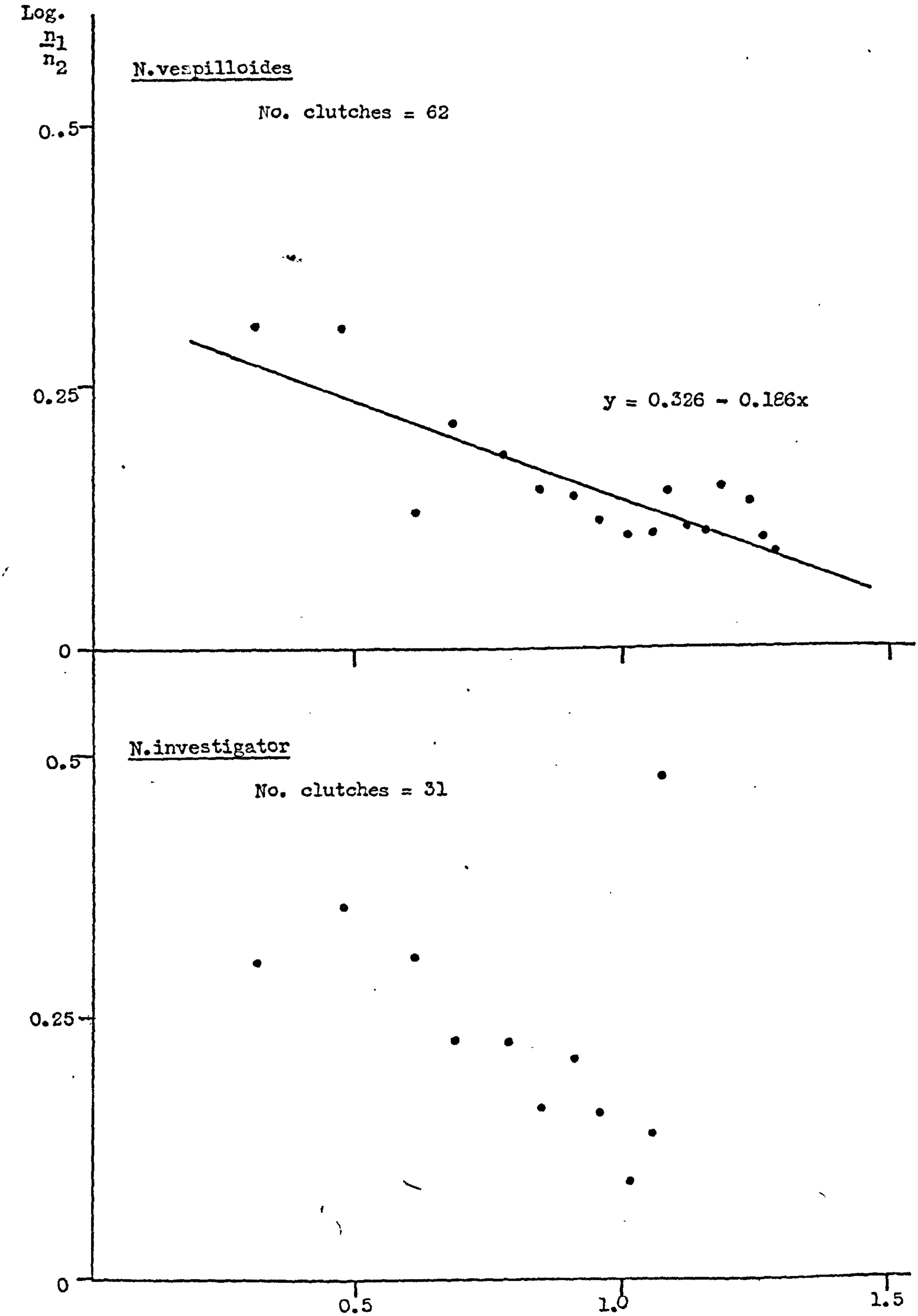

Log. n1/n2
N.vespilloides
No. clutches = 62
0.5
0.25
0
y = 0.326 - 0.186x
N.investigator
No. clutches = 31
0.5
0.25
0
0.5
1.0
1.5
Log. no. I / clutch

Table 4:16.

Range of variation in clutch size caused by transplant experiments.

	Number of corpses	variation in size of clutch	size of clutch $\bar{x}$	SD
N.vespilloides				
Field (first instar)				
Normal range (control)	82	2 - 22	13.32	4.87
Experimental range	178	2 - 40	14.00	10.74
Laboratory (egg)				
Normal range (control)	62	3 - 24	13.39	4.98
Experimental range	140	2 - 44	15.37	8.04
N.investigator				
Field (first instar)				
Normal range	41	3 - 10	7.07	1.92
Experimental range	93	2 - 24	9.67	5.32
Laboratory (egg)				
Normal range	39	2 - 10	6.20	1.92
Experimental range	80	3 - 22	8.32	5.34

Clutch mortality in transplant experiment controls was not significantly different from that observed during other experiments (c.f. figs 4:10, 4:11) (Table 4:17). This suggests that the techniques used in the transplant experiments do not significantly affect developmental mortality. Any change in mortality in experimental corpses is, therefore, likely to be a result of alteration in number of eggs or first instar larvae. For analysis of relationships between the variables measured, clutch size was compared with: (a) overall mortality, (b) mortality at dispersal and (c) mean larval weight at dispersal. As before mortality is expressed as $\log \frac{n_1}{n_2}$.

(a) Clutch size and overall developmental mortality.

There is similar variation of mortality with density in both laboratory and field (figs. 4:12, 4:13). Field mortality varies at a higher level, as expected from earlier results. There is a sharp increase in mortality at a threshold egg or larval density (N_c), defined as the intercept on the x-axis of the regression line through the highest values of the relationship. The difference between N_c in field and laboratory is the equivalent of about 3% egg mortality. Overall mortality in the field does not include this figure, but if it is added, the estimates of threshold density from field and laboratory are found to be similar.

In none of the control corpses did clutch size exceed N_c. Mortality of control clutches and experimental clutches smaller than the threshold density varies, but did not increase significantly with egg or larval density (Table 4:18). In all cases, the observed b values are not significantly different from a slope of $b = 0$ at $p = 0.05$, and so mortality in control clutches and in experimental clutches smaller than threshold density is not density dependent. As the overall mortalities were similar (Table 4:19) as well as the slopes of the regression lines, control clutches and experimental clutches smaller than the threshold

Table 4:17

Comparison of developmental mortality in transplant control and normal corpses (figs. 4:13, 4:14).

	Number of corpses	Clutch size	Total number mature adults	% mortality
Laboratory		(egg)		(egg-adult)
N .vespilloides				
transplant experimental control	62	820	710	13.41
normal clutches	201	2440	2113	12.58
	$\chi^2 = 0.000$ doff 1 $p > 0.05$			
N.investigator				
transplant experimental control	39	242	189	21.90
normal clutches	42	284	231	18.67
	$\chi^2 = 0.096$ doff 1 $p > 0.05$			
Field		(first instar)		(first instar - adult)
N.vespilloides				
transplant experimental control	82	1092	836	23.44
normal clutches	62	643	483	24.88
	$\chi^2 = 0.063$ doff 1 $p > 0.05$			
N.investigator				
transplant experimental control	41	290	196	32.41
Normal clutches	31	207	133	35.75
	$\chi^2 = 0.122$ doff $p > 0.05$			

Fig. 4:12

Developmental mortality during transplant experiments (laboratory) : Relationship between clutch size and mortality

n_1/n_2 as in fig. 4:10

—•— = mortality in experimental clutches

O = mortality in control clutches

/‾‾‾ = range of mortality in normal clutches

n_c = threshold

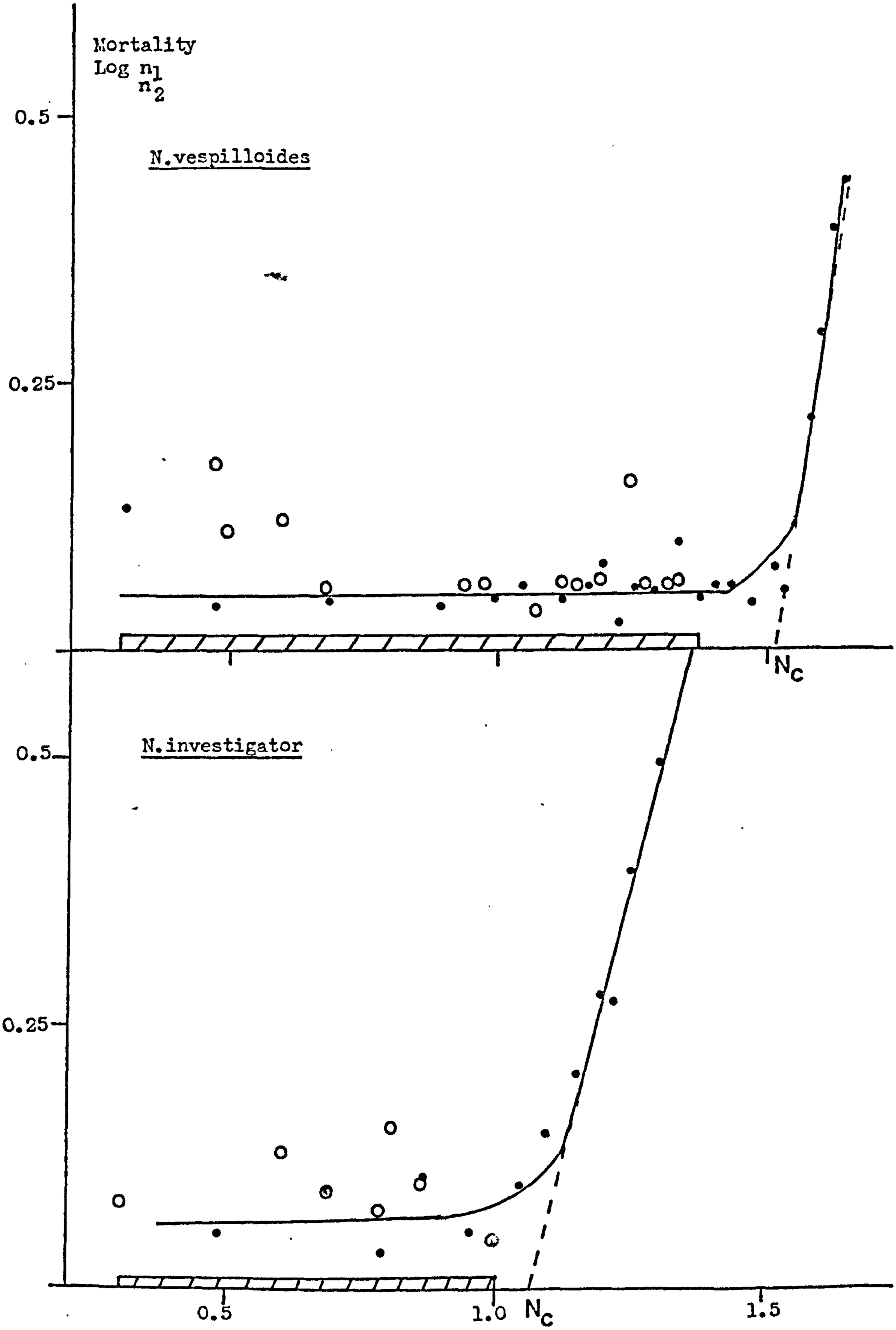

Mortality
Log $\frac{n_1}{n_2}$
0.5
0.25
N.vespilloides
0.5
0.25
N.investigator
0.5
1.0
N_c
1.5
Log No. Eggs/ clutch.

Fig. 4:13

Developmental mortality during development (field) :

Relationship between clutch size and mortality

n_1/n_2 as in fig. 4:11

Remaining symbols as in fig. 4:12

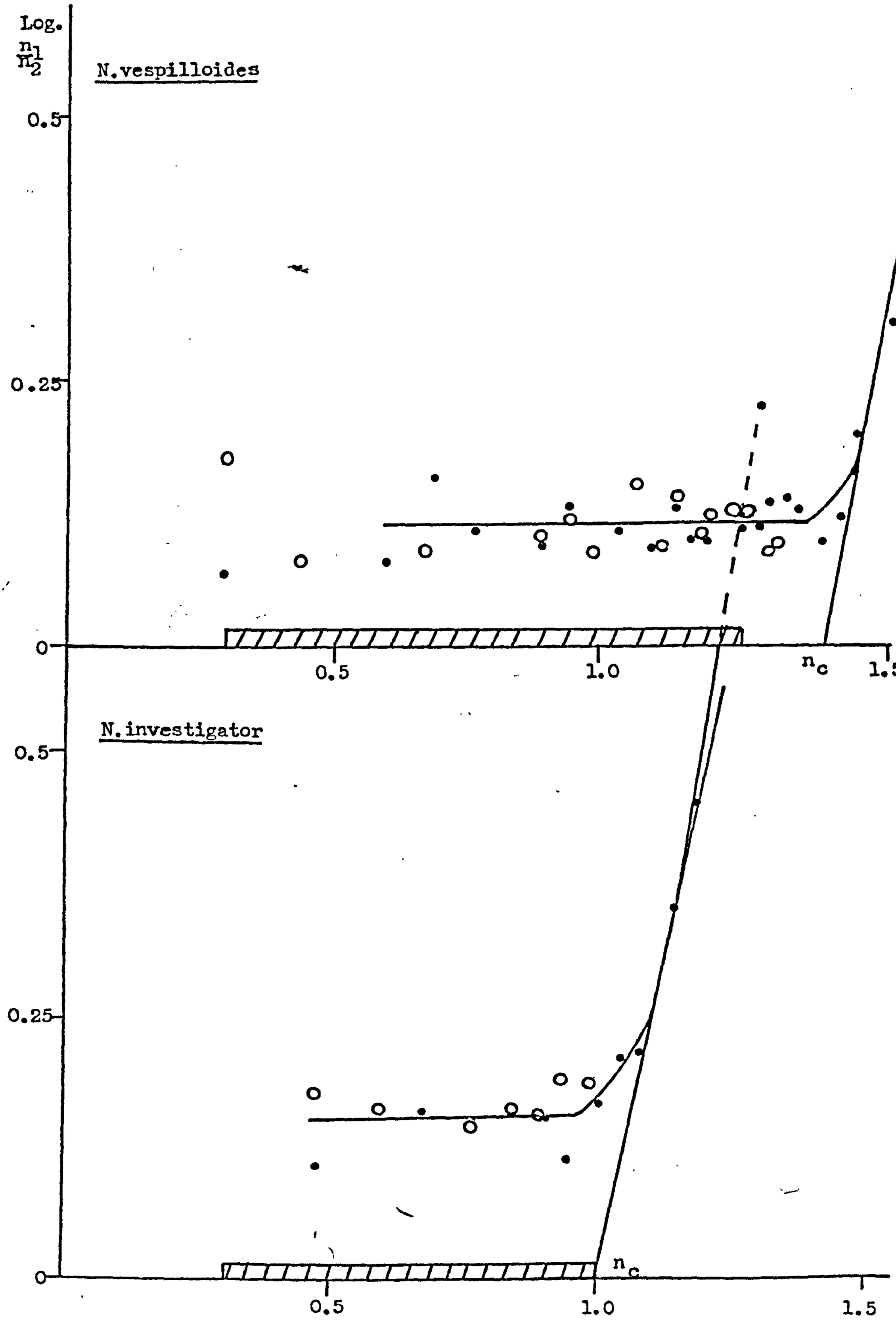

Log. $\frac{n_1}{n_2}$
N.vespilloides
0.5
0.25
0
0.5
1.0
n_c
1.5
N.investigator
0.5
0.25
0
0.5
1.0
n_c
1.5
Log no. first instar / clutch.

Table 4:18

Relationships between clutch size and developmental mortality in control clutches and experimental clutches smaller than the threshold density.

Experimental condition	b	r	doff	p
N.vespilloides				
Laboratory control	-0.059	-0.360	14	>0.05
" $< N_c$	-0.030	-0.413	15	>0.05
Field control	-0.021	-0.236	13	>0.05
" $< N_c$	0.031	0.392	16	>0.05
N.investigator				
Laboratory control	-0.000	-0.000	5	>0.05
" $< N_c$	-0.024	-0.165	4	>0.05
Field control	0.020	0.218	5	>0.05
" $< N_c$	0.208	0.898	5	>0.05

Table 4:19

Comparison of developmental mortality in control clutches and in experimental clutches smaller than threshold density.

Experimental Condition	Number of clutches	Total number eggs	adults	% adults
Laboratory				
N.vespilloides				
Control	62	820	710	13.41
$< N_c$	116	2040	1882	7.75
	($\chi^2 = 1.102$ doff 1 $p > 0.05$)			
N.investigator				
Control	39	242	189	21.90
$< N_c$	25	167	141	15.57
	($\chi^2 = 0.270$ doff 1 $p > 0.05$)			
Field		First instar	adults	
N.vespilloides				
Control	82	1092	836	23.44
$< N_c$	144	2174	1685	22.49
	($\chi^2 = 0.048$ doff 1 $p > 0.05$)			
N.investigator				
Control	41	290	196	32.41
$< N_c$	34	220	161	26.82
	($\chi^2 = 0.328$ doff 1 $p > 0.05$)			

density were considered similar for the purposes of fig. 4:12 and 4:13, and only one line was drawn to describe the relationship between clutch size and larval mortality in both.

Mortality increases sharply in experimental clutches larger than the threshold density (figs. 4:12, 4:13). There is a significant correlation between egg density and mortality in all cases (N.vespilloides: field, $r = 0.979$, d.of f. 3, $p < 0.01$, laboratory, $r = 0.979$, d.of f. 4, $p < 0.001$; N.investigator: field, $r = 0.968$, d.of f. 6, $p < 0.001$, laboratory, $r = 0.969$, d.of f. 6, $p < 0.001$). The slopes of the regression lines through these points are : N.vespilloides, field, $b = 2.44$, laboratory, $b = 2.78$; N.investigator, field, $b = 2.38$, laboratory, $b = 1.70$. The slopes of the regression lines are significantly different from a slope of $b = 0$, and so there is a density dependent relationship between clutch size and larval mortality in clutches larger than the threshold density.

On 25gm corpses, density dependent mortality occurs above a threshold density of 33 eggs for N.vespilloides and 11 eggs for N.investigator. Normally N.vespilloides and N.investigator lay no more than 24 and 10 eggs respectively on 25gm corpses (Table 4:16). Density dependent mortality is, therefore, unlikely to occur normally in either species as the number of eggs laid is less than the threshold density required to cause such a mortality. The threshold for N.investigator is smaller than that for N.vespilloides, suggesting that fewer N.investigator larvae can live on a 25gm corpse if density dependent mortality is to be avoided.

(b) Clutch size and mortality at dispersal.

There was no correlation between clutch size and mortality at dispersal either in control clutches or experimental clutches, whether

smaller or larger than the threshold density, Mortality at dispersal was uniformly low, and was not density dependent, as the slopes of all regression lines were not significantly different from b = 0. This suggests that the density dependent mortality factor acting in clutches larger than the threshold density must take effect after dispersal from the corpse, i.e. during the prepupal or pupal periods. As most mortality occurs during these stages normally (Tables 4:11, 4:14) any major mortality factor could be expected to act then.

(c) Clutch size and mean larval weight at dispersal.

There is wide variation in mean larval weight at dispersal in control clutches and in experimental clutches smaller than threshold density (figs. 4:14, 4:15). There is no correlation between egg numbers and mean larval weight at dispersal in these clutches and slopes of regression lines are not significantly different from slopes of b = 0.

In clutches larger than the threshold density, there is a significant negative correlation between clutch size and MLWD (N.vespilloides : laboratory, $r = -0.987$, d.of f. 4, $p < 0.001$, field, $r = -0.915$, d.of f. 3, $p < 0.05$; N.investigator, laboratory, $r = -0.954$, d.of f. 4, $p < 0.001$, field $r = -0.981$, d.of f. 6, $p < 0.001$). The slopes of all regression lines are significantly different from a slope of b = 0 at p = 0.05. In all cases, therefore, there is an inverse density dependent relationship between MLWD and clutch size in clutches larger than threshold density.

There is a rapid drop in mean larval weight at dispersal at the threshold density, which may represent a critical point in the relationship between number of larvae and the food available for their consumption. Although no experiments were carried out to test if decreased larval weight actually caused the mortality observed in clutches

Fig. 4:14

Relationship between clutch size and mean larval weight at dispersal (laboratory)

Symbols as in fig. 4:12

Log. MLWD

N. vespilloides

	r	d. of f.	p
control	0.095	14	>0.05
$<n_c$	0.254	15	>0.05

$y = 4.991 - 1.799x$

N. investigator

	r	d. of f.	p
control	0.338	5	>0.05
$<n_c$	0.254	4	>0.05

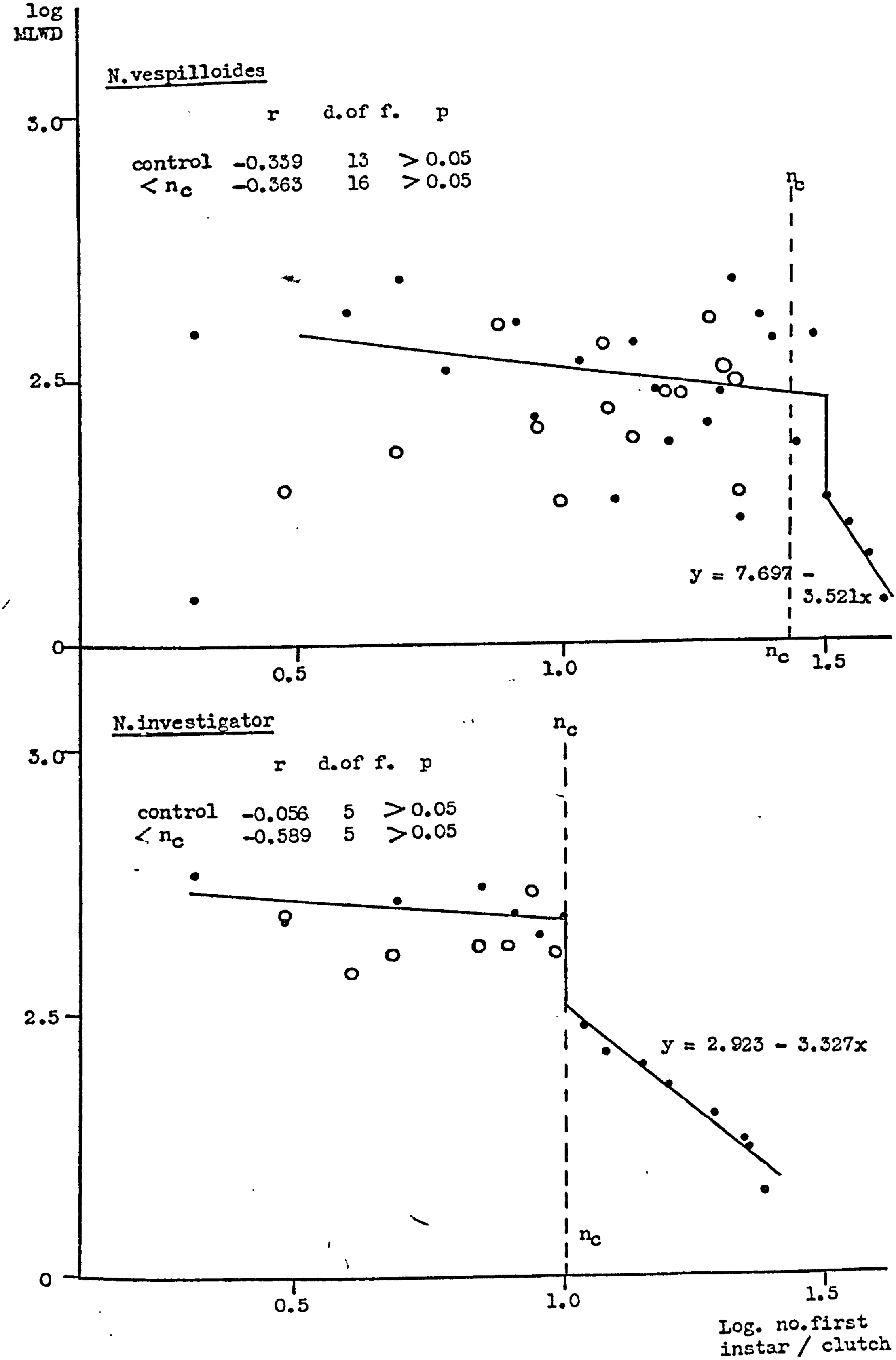
$y = 3.156 - 3.734x$

Log. no. eggs/ clutch

Fig. 4:15

Relationship between clutch size and mean larval weight at dispersal (field).

Symbols as in fig. 4:12


log MLWD
N.vespilloides
r d.of f. p
control -0.339 13 > 0.05
< n_c -0.363 16 > 0.05
n_c
y = 7.697 - 3.521x
3.0
2.5
0
0.5
1.0
n_c
1.5
N.investigator
r d.of f. p
control -0.056 5 > 0.05
< n_c -0.589 5 > 0.05
n_c
y = 2.923 - 3.327x
3.0
2.5
0
0.5
1.0
n_c
1.5
Log. no.first instar / clutch

larger than threshold density, consideration of some mortality factors suggests that this might be the case. The slopes of the regression lines for clutch size and mortality are the same in field and laboratory (figs. 4:12, 4:13) (N.vespilloides, $F = 2.76$, d.of f. 1.7, $p > 0.05$; N.investigator, $F = 0.45$, d.of f. 1.12, $p > 0.05$), although the elevations of the lines are significantly different (N.vespilloides, $F = 85.88$, d.of f. 2.8, $p < 0.001$); N.investigator, $F = -114.21$, d.of f. 1.13, $p < 0.001$). Therefore a density dependent mortality factor acts at the same rate in both field and laboratory. As mortality occurs in the laboratory, it is unlikely to be due to predation or parasitism. Weather may not be a density dependent mortality factor (Klomp, 1962). Therefore, the observed density dependent mortality may be due to some intrinsic factor such as larval or pupal starvation, or failure to moult successfully. Both of these could be affected by variations in larval weight, and so a decrease in larval weight could be responsible for increased mortality.

Comparison of figs. 4:12 and 4:13 shows that the mortality in the field is higher than that in the laboratory by a factor which is constant, irrespective of clutch size, i.e. is density independent. This mortality, only occurring in the field may be caused by several factors, including predation, parasitism and weather but it is not known in what combinations they may occur.

In a second series of transplant experiments, the relationship between clutch size, threshold density corpse size and larval mortality was analysed further.

(a) Reduction in size of corpse, clutch size and larval mortality.

In these experiments, only N.vespilloides were used. Experiments were carried out in the field and first instar larvae were

transplanted. Corpses were put into flowerpots and were not disturbed after the transplant. The only variable recorded was the number of callow adults. Sixty mice of 15gm $\pm$ 1gm were used, 60 of 10gm $\pm$ 0.5gm and 60 of 5gm $\pm$ 0.5gm (light mice). Ten of the buried corpses of each size were treated as controls, the remainder as experimental corpses. Mortality in control clutches (Table 4:20) was not significantly different from that observed in normal clutches (Table 4:14) (15gm : $\chi^2 = 0.574$, d.of f. 1, $p > 0.05$; 10gm : $\chi^2 = 0.426$, d.of f. 1, $p > 0.05$; 5gm : $\chi^2 = 0.038$, d.of f. 1, $p > 0.05$). As in other transplant experiments, experimental procedure did not have any effect on mortality.

The relationship between larval density and mortality in corpses less than 25gm is very similar to that in 25gm corpses (figs. 4:16, 4:17). Below a threshold density in experimental corpses and in control corpses, the slopes of regression lines are not significantly different from $b = 0$, and so mortality is density independent. Above a threshold density, the slope of the regression line is significantly different from $b = 0$. In all cases, therefore, density dependent mortality occurs above a threshold larval density.

Above the threshold density, the slope of the regression line for 25gm corpses is not significantly different from that observed on 15gm ($F = 0.123$, d.of f. 1,6, $p > 0.05$), 10gm ($F = -0.442$, d.of f. 1,7, $p > 0.05$) or 5gm corpses ($F = 0.010$, d.of f. 1,6, $p > 0.05$). Therefore despite the differences in size of corpse and number of larvae, the rate of mortality is the same in each case. Control clutches are the same size on 25gm and 15gm corpses ($r = 0.581$, d.of f. 90, $p > 0.05$), but are significantly smaller on 10gm ($r = 2.343$, d.of f. 90, $p < 0.05$) and 5gm corpses ($r = 3.211$, d.of f. 90, $p < 0.01$) (Table 4:20). There is a significant correlation between corpse size and mean clutch size ($r = 0.986$,

Table 4:20.

Effect of corpse size on larval mortality (N.vespilloides)

		Corpse size (gms)			
		25	15	10	5
% mortality (controls)		23.44	15.60+	16.30+	22.22+
number of larvae/corpse (controls)	$\bar{x}$	13.22	11.36+	9.2 *	8.1**
	± SD	± 4.87	± 5.697	± 6.989	± 3.635
range of first instar per corpse (controls)		3 -22	3 -22	2 -20	2 -15
threshold-number first instar/corpse (experimental)		27.54	23.4	26.3	19.00
difference between threshold and maximum number of larve in controls		c 5	c 1	c 6	c 4

\+ Not significantly different from 25gm corpse at $p = 0.05$

* Significantly different from 25gm corpse at $p < 0.05$

** Significantly different from 25gm corpse at $p < 0.01$

Fig. 4:16

Relationships between clutch size and mortality in corpses of less than 25gms. :

N.vespilloides, field

n_1/n_2 as in fig, 4:11

Remaining symbols as in fig. 4:12

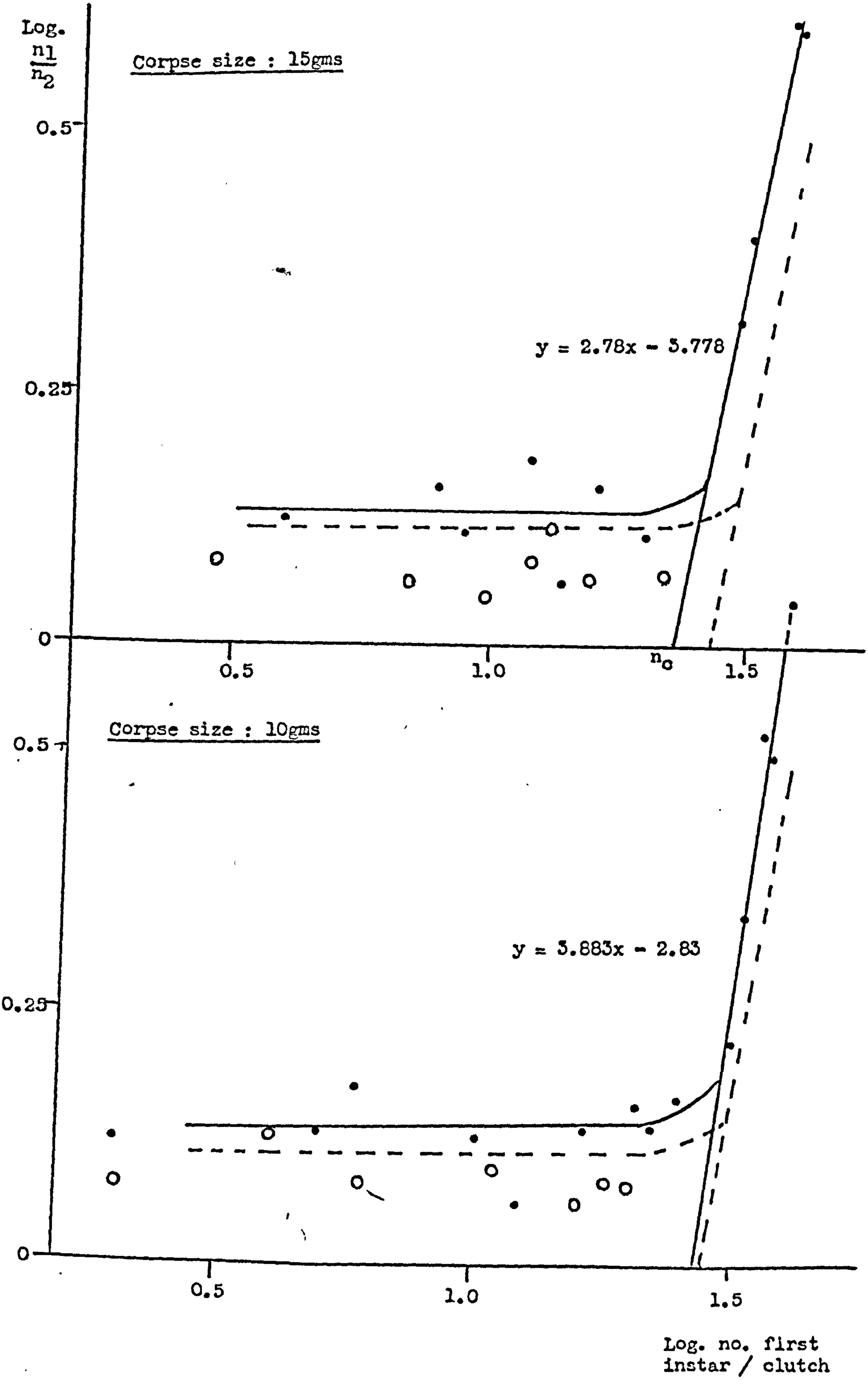

Log. n1/n2
Corpse size : 15gms
0.5
0.25
0
y = 2.78x - 5.778
0.5
1.0
no
1.5
Corpse size : 10gms
0.5
y = 3.883x - 2.83
0.25
0
0.5
1.0
1.5
Log. no. first instar / clutch

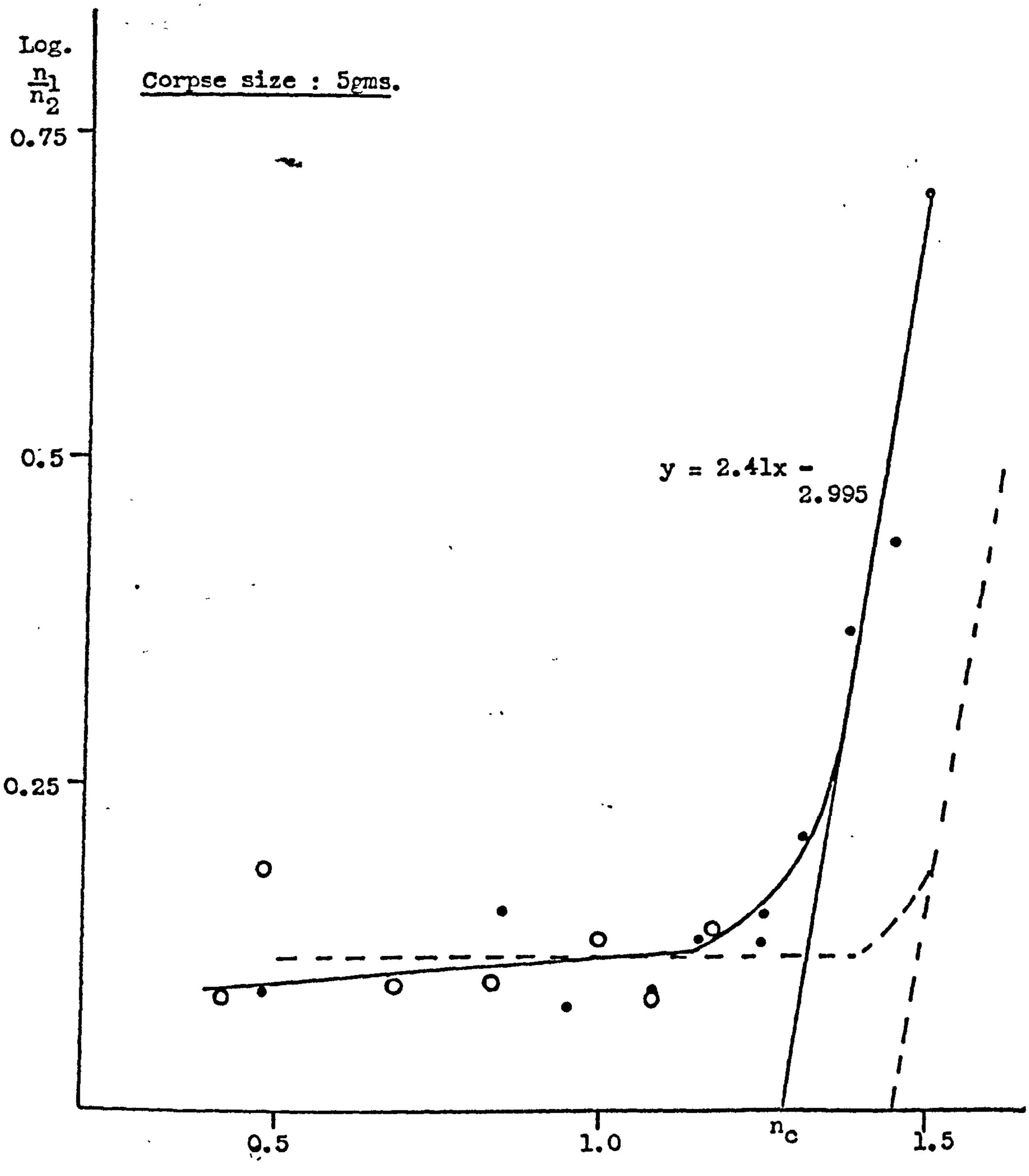
Fig. 4:17

Relationship between clutch size and mortality in corpses of less than 25gms. (Contd.)

N.vespilloides : Field

n_1/n_2 as in fig. 4:11

Remaining symbols as in fig. 4:12


Log. $\frac{n_1}{n_2}$
Corpse size : 5gms.
0.75
0.5
0.25
y = 2.41x - 2.995
0.5
1.0
n_c
1.5
Log. no. first instar / clutch

d.of f. 2, $p < 0.02$), over the range of corpse sizes used in these experiments (fig. 4:18). No correlation was found between clutch size and mortality using corpses greater than 10gm in size in the laboratory (fig. 4:3). Although representing a very limited range of corpse size, fig. 4:18 suggests that such a relationship may be observed when corpses of less than 10gm are used. A similar relationship was observed for N.investigator in the laboratory over a wide range in corpse sizes (fig. 4:4). Both species may show a reduction in clutch size below a particular size of corpse; for N.vespilloides this may be about 10gm and for N.investigator at some point heavier than 30gm. Decreases in clutch size on smaller corpses are not accompanied by changes in developmental mortality (Table 4:20).

Different corpse sizes have different threshold densities (Table 4:18), the threshold density decreasing from 25gm to 5gm corpses. The relationship between corpse size and threshold density is not significant (correlation coefficient, $r = 0.763$, d.of f. 2, $p > 0.05$; Kendall's rank correlation, $r = 0.667$, $n = 4$, $p > 0.33$), possibly because of the small number of replicates.

The number of larvae normally found on corpses of all sizes (for example, control clutches) is less than the density at which mortality begins (i.e. threshold density). A decrease in threshold density, as occurs for N.vespilloides on corpses less than 10gm, is associated with a decrease in mean clutch size, but no change in mortality. It is possible that the observed reduction in clutch size may be a response to the reduced threshold density (= carrying capacity of the corpse), thereby preventing density dependent mortality. It must be emphasised however, that as far as normal clutches are concerned, the threshold density does not exist. The larval density actually observed

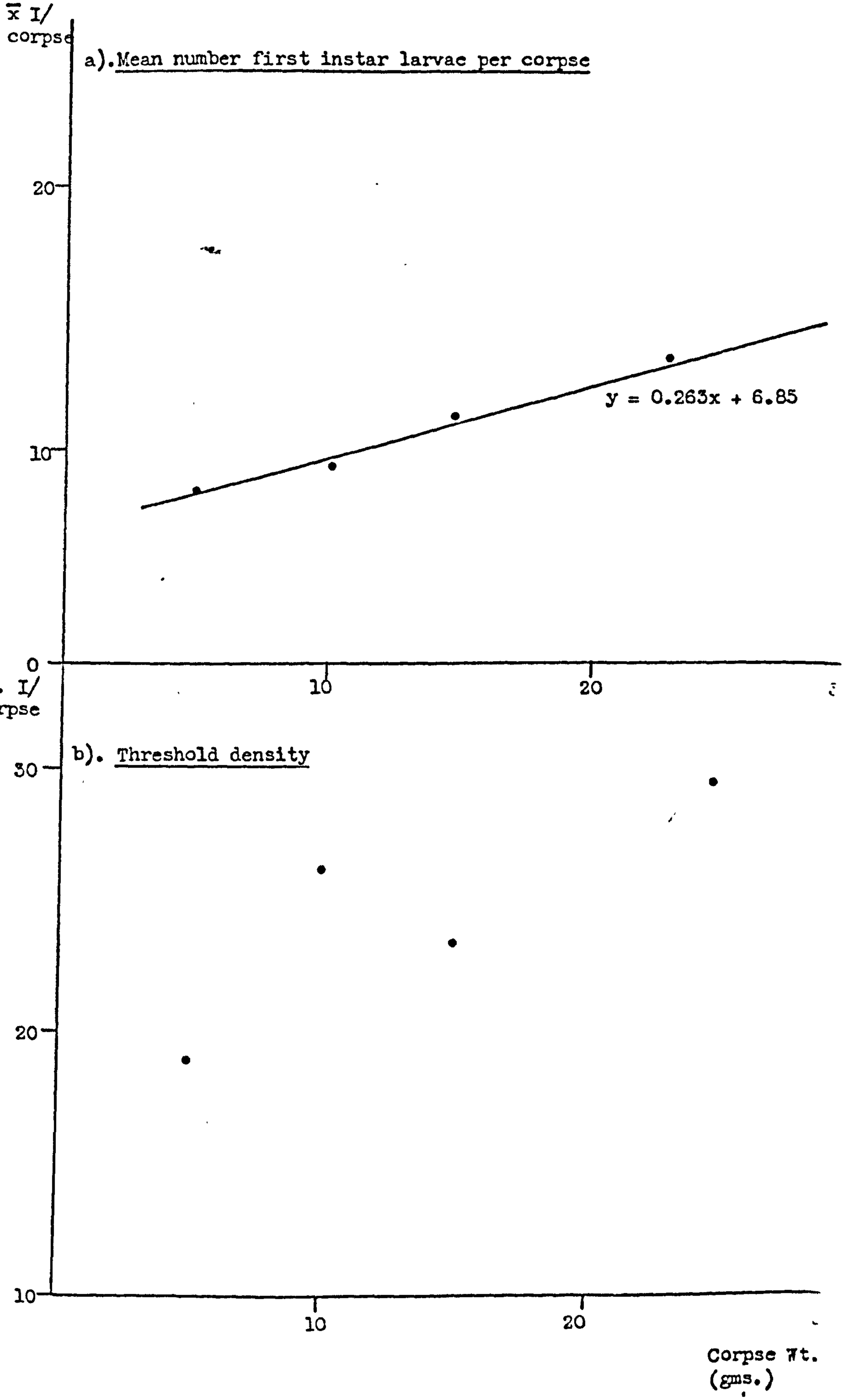
Fig. 4:18

Relations between size of corpse and

a) mean number of first instar larvae per corpse

b) threshold density

a). Mean number first instar larvae per corpse



b). Threshold density

is always less than the threshold density, which is demonstrable, only under experimental conditions.

(b) Increase in size of corpse, clutch size and larval mortality.

Transplant experiments were carried out on rats to increase corpse size. The same range of larval numbers was used as in mice (Table 4:16). Mortality in experimental corpses remained at the same level as control corpses, regardless of clutch size. Crude extrapolation from fig. 4:18 suggested that the threshold density for a rat of 150gms might be about 100 larvae per corpse. Below this, no change in mortality would be expected. Accordingly, several transplants were carried out using large numbers of larvae ($>$ 100/corpse), taken from other experiments. Six corpses were used, and in all of them there was major larval mortality. This mortality may have occurred because the single female on each corpse was unable to feed 100 larvae. Mortality of this type occurred at lower clutch densities than the assumed threshold density, which was not observed.

Three observations made during field experiments provide supporting evidence for the hypothesis that threshold density varies with corpse size, and is associated with variations in clutch size.

(a) Multiple clutches.

On several occasions, large numbers of larvae were counted on rat corpses. Investigation showed that in these cases, several independent clutches were present on the same corpse, each with a separate female in attendance. Often one clutch was found at the head and one at the tail of the corpse. Such behaviour has been noted before on snakes (Milne and Milne, 1976).

Multiple N.vespilloides corpses were recorded from five rat corpses and multiple N.investigator clutches from three rats (Table 4:21).

Table 4:21

Multiple clutches found during 1974 and 1975

Weight of corpse (gms)	Number of larvae	Number ♀♀ (minimum number of clutches)
N.vespilloides		
261	96	4
103	84	4
156	98	4
307	152	6
138	42	2
N.investigator		
143	35	2
332	146	5
211	136	5

Although the survival of these clutches was not measured, observations suggested that mortality was similar to that recorded in other corpses. Therefore rat corpses can support large numbers of burying beetle larvae before density dependent mortality occurs. The number of N.vespilloides actually found on rats (Table 4:21) is similar to that predicted by crude extrapolation of threshold densities in fig. 4:13 - i.e. about 100 larvae on a corpse of 150gms.

(b) Abnormal corpses.

The number of larvae at dispersal was recorded on some abnormal corpses and compared with that observed on normal mice and rats (Table 4:22). Despite differences in volume and weight between different types of corpse, the number of larvae produced in each is similar, except when the number of N.investigator larvae produced on mice is compared with that produced on supermice and light rats.

Whatever the effect of corpse size on egg number and threshold density, it appears to involve more than one aspect of size. For N.investigator the increase in corpse weight from mice to supermice and light rats may have raised the threshold density, thereby allowing more eggs to be laid. However, changes in weight and volume between supermice, light rats and rats have no effect. No effects were observed for N.vespilloides possibly because the threshold density in each case is greater than the number of eggs actually laid.

(c) Breeding on mice by N.humator

N.humator buried 7 mice at Rossdhu (Table 3:4). The mean number of third instar larvae on these corpses was 4.57 ± 2.637. If the life tables of N.vespilloides and N.investigator are applicable to N.humator, this means that the number of eggs laid was about 5. A mature female N.humator has 11.00 ± 2.323 eggs (Table 2:6). This suggests that

Table 4:22

Number of larvae produced at dispersal on abnormal corpses

Corpse	Mean Corpse Weight (gms).	N.vespilloides			N.investigator		
		Number at dispersal		No. Clutches	Number at dispersal		No. clutches
		$\bar{x}$	SD		$\bar{x}$	SD	
supermice	92	12.71	3.834	39	7.82	5.114	46
light rats	101	12.62	2.612	20	8.34	3.283	30
mice	25	12.39	4.332	144	6.22	1.164	80
rats	150	12.28	3.310	39	9.44	3.251	18

Differences between means:

N.vespilloides

Corpses	r	doff	p
supermice:light rats	0.094	57	> 0.05
mice : supermice	0.550	181	> 0.05
mice : light rats	0.332	162	> 0.05
rats : supermice	0.407	76	> 0.05
rats : light rats	0.222	57	> 0.05

N.investigator

supermice:light rats	0.494	74	> 0.05
mice : supermice	2.687	124	< 0.05
mice : light rats	5.024	108	< 0.001
rats : supermice	1.246	62	> 0.05
rats : light rats	1.106	46	> 0.05

either not all the mature eggs are laid on these corpses or that larvae mortality in N.humator is much heavier than in N.vespilloides or N.investigator. Which of these is true cannot be proved from the data available, but it is clear that mouse corpses are much smaller than the type of corpse preferred by N.humator and will presumable have a much lower threshold density.

The experiments described in this section suggest that one source of variation in clutch size may be a response to corpse size. Below a certain corpse size, clutch size must be reduced to prevent density dependent mortality.

4.3.1.4. Corpse temperature.

The temperature in the corpse was measured to estimate the stability of the environment for burying beetle larvae. 48 mice buried by N.vespilloides were used. Readings of temperatures in the crypt and the soil adjacent to each corpse were made, and air temperature was recorded. Temperatures were measured at noon and at midnight. The average depth of burial was 4.6 ± 1.27 cm.

Daily fluctuations in temperature were greatest in the air, less in the soil and crypt and least in the corpse (fig. 4:19), a mean daily range of temperatures of $9.4^{\circ}C$ in the air being reduced to $2.64^{\circ}C$ in the corpse (Table 4:23). Both crypt and corpse remain at a higher temperature than the surrounding soil (Table 4:23). Differences in mean temperatures between crypt and soil are significant (noon, $r = 2.475$, d.of f. 14, $p < 0.05$; midnight, $r = 4.060$, d.of f. 14, $p < 0.01$) as are those between corpse and soil, (noon, $r = 5.135$, d.of f. 14, $p < 0.001$; midnight, $r = 3.69$, d.of f. 14, $p < 0.01$). At noon the corpse is the same temperature as both crypt ($r = 1.917$, d.of f. 14, $p > 0.05$) and air

Fig. 4:19

Daily fluctuations in temperature in corpses buried by *N.vespilloides* in the laboratory

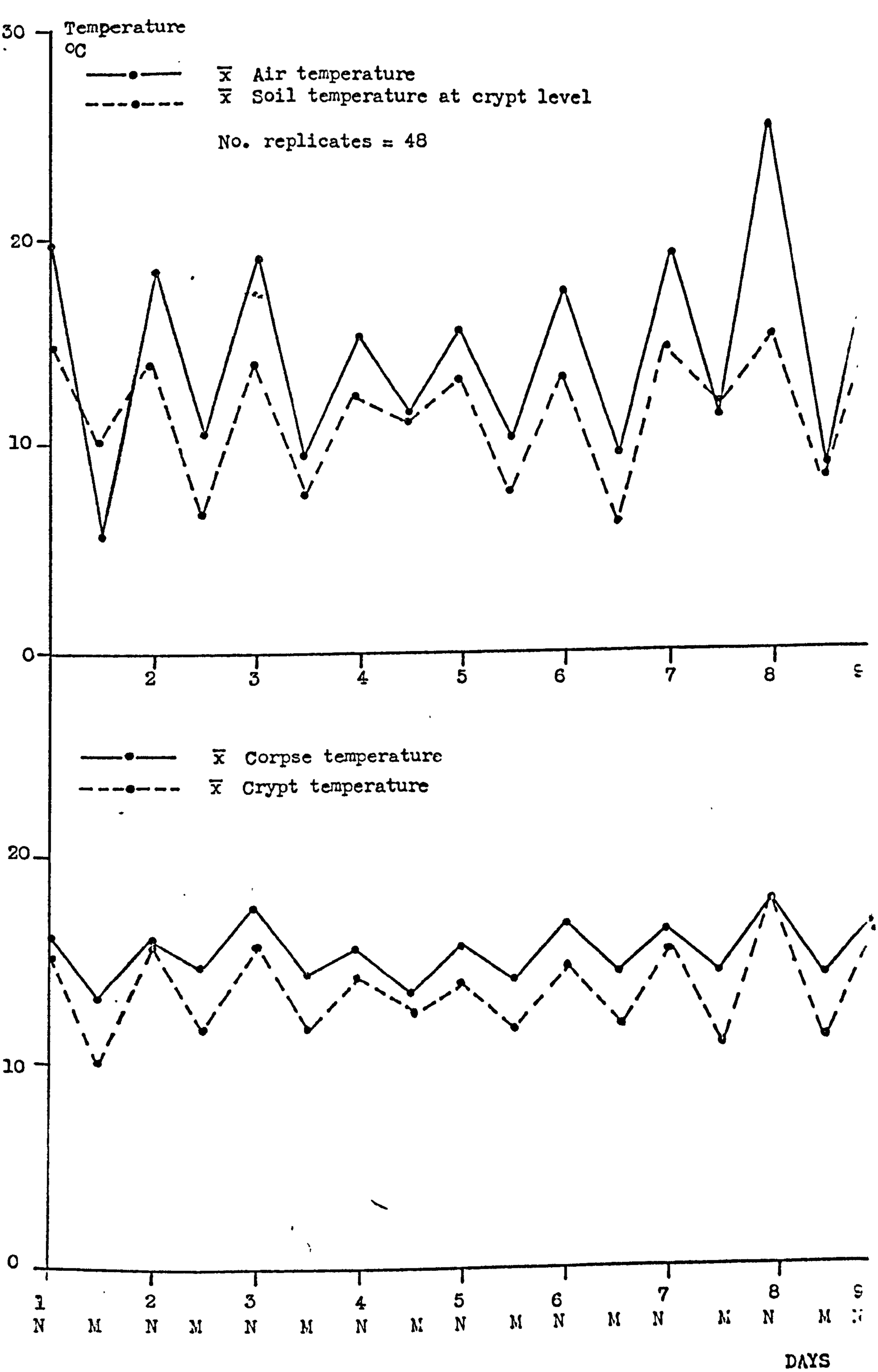

Temperature
°C
$\bar{x}$ Air temperature
$\bar{x}$ Soil temperature at crypt level
No. replicates = 48
30
20
10
0
2
3
4
5
6
7
8
$\bar{x}$ Corpse temperature
$\bar{x}$ Crypt temperature
20
10
0
1
2
3
4
5
6
7
8
N
M
DAYS

Table 4:23

Temperature fluctuations in air, soil, crypt and corpse in the laboratory (Summary)

Location	Temperature °C noon $\bar{x}$	SD	midnight $\bar{x}$	SD	Daily range in temperature °C $\bar{x}$	SD
air	18.82	3.123	9.412	1.979	9.40	4.552
soil at crypt level	14.21	1.106	8.30	2.166	5.66	2.106
crypt	15.70	1.292	11.64	0.852	4.07	1.899
corpse	16.75	0.855	14.11	0.437	2.64	0.966

(No. replicates at each location - 48)

Significance of differences in mean daily range of temperatures (student's t test).

	air	soil	crypt	corpse
air	-			
soil	>0.05	-		
crypt	<0.01	>0.05	-	
corpse	<0.01	<0.01	>0.05	-

($r = 1.808$, d.of f. 14, $p > 0.05$). However at midnight, the corpse is warmer than the air ($r = 6.599$, d.of f. 14, $p < 0.001$) and the crypt ($r = 7.302$, d.of f. 14, $p < 0.001$).

These observations suggest that the crypt may act as a buffer for the corpse against temperature fluctuations in the air and the soil. At night, the temperature of the crypt is higher than that of the air, due perhaps to radiation of larval metabolic heat from the corpse into the crypt. By providing a surrounding of warmer air, the crypt may slow down loss of heat from the corpse to the soil, thereby maintaining the corpse at a higher temperature than the soil and air. During the day, the crypt does not heat up as much as the air. The crypt may absorb heat from the air before it reaches the corpse, again cushioning the corpse against external influences. As it is still cooler than the corpse, the crypt may absorb larval metabolic heat, thereby preventing a build up of heat in the corpse.

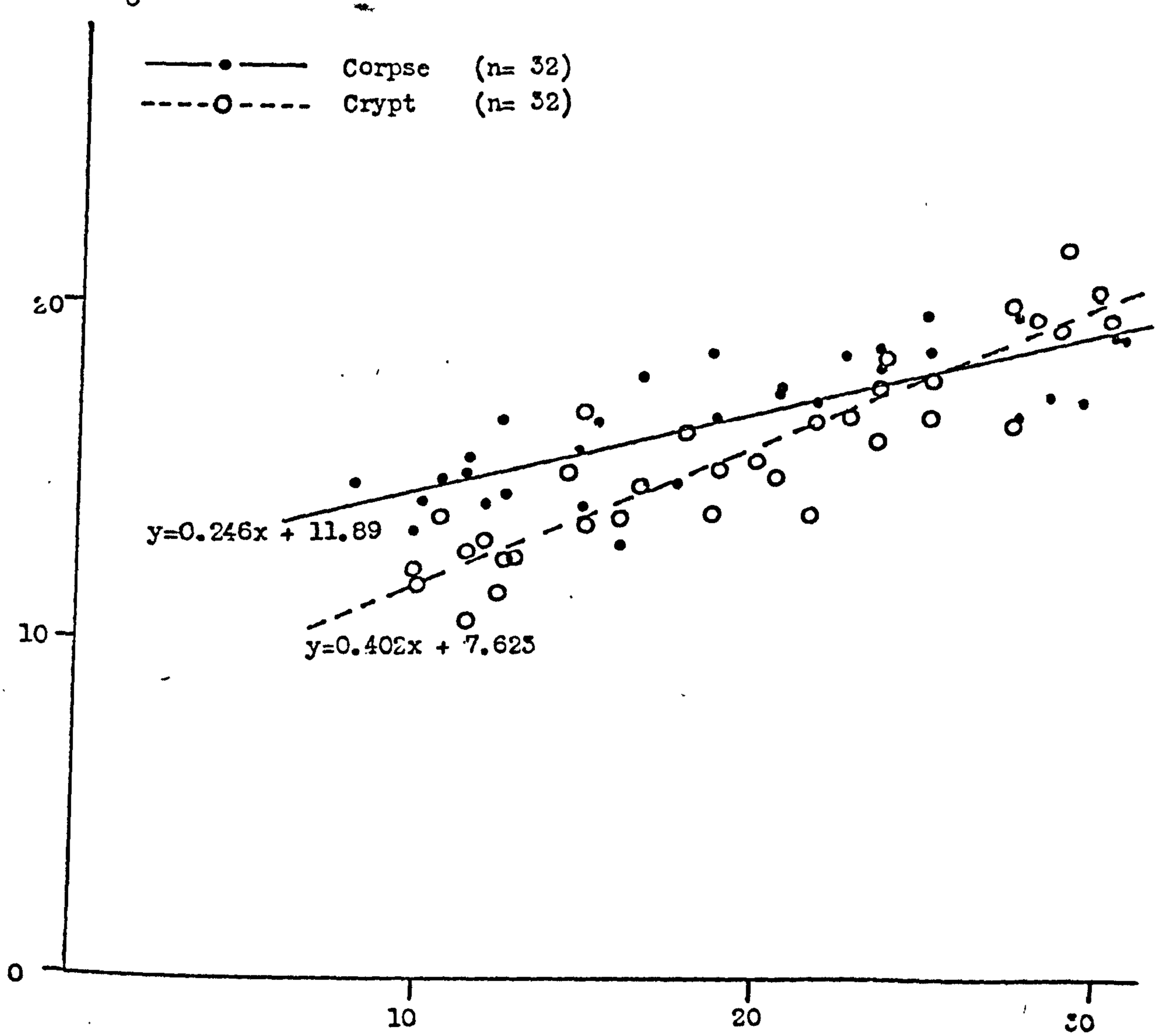
The relationship between air temperature and temperatures in crypt and corpse was assessed by random measurement. There is a correlation between temperature and crypt temperature ($r = 0.897$, d.of f. 30, $p < 0.001$), and between air temperature and corpse temperature ($r = 0.787$, d.of f. 30, $p < 0.001$) (fig. 4:20). The slope of the crypt/air temperature relationship is greater than that of the corpse/air temperature relationship ($F = 9.484$, d.of f. 1,60, $p < 0.01$), while the reverse is true of the elevations of the regression lines ($r = 15.586$, d.of f. 1,61, $p < 0.01$). The corpse is generally warmer than the crypt (c.f. fig. 4:20) and remains relatively cooler at high air temperatures and warmer at low air temperatures. This supports the hypothesis that the crypt is acting as a buffer for the corpse.

Fig. 4:20

Relations between air temperature and temperatures in the corpse and crypt.

Mean temperature
°C

——•—— Corpse (n= 32)
----o---- Crypt (n= 32)



Air temperature
°C

Although the crypt may act as a buffer, temperatures in the corpse varies with fluctuations in air temperatures, albeit at a lower level. This may occur because the corpse is not buried deep enough in the laboratory to avoid the effect of fluctuation in air temperature. Field observations do not support this hypothesis however. Depth of burial in the field varied from 2 - 9cm, with a mean of 4.3cm (n = 44), suggesting that the depth of burial observed in the laboratory is normal. This would imply that fluctuations in temperature might occur in the field. Some crude temperature measurements in the field suggested that corpses were about 1°C cooler than the air during the day, mean corpse diurnal temperature being 15.98°C and mean air temperature 16.73°C (n = 30). The laboratory results may therefore reflect the field conditions, although fluctuations in temperature in the field will be affected by many factors not present in the laboratory, for example, the insulating effect of leaf litter.

Mean corpse temperatures were similar in field and laboratory at about 16°C. It is of interest to note that Théorides and Van Heerdt (1952) showed that the preferred temperatures of N.humator were from 11 - 21°C with a mean of 16.32°C, while N.vespillo preferred a range from 11 - 23°C with a mean of 16.94°C. Springett (1967) conducted growth experiments at temperatures varying from 15 - 20°C with a mean of 16°C but did not explain why. Therefore, the observed results may be generally applicable and may reflect normal field conditions.

4.3.2. Relations Between Adults and Food.

4.3.2.1. Feeding prior to breeding.

Not enough overwintered adults were available to analyse the relationship between food and maturation of gonads. Therefore, most of the adults available were used in baseline studies of survival with and

without food. These experiments are of relevance to the breeding of Necrophorus as a beetle must feed to survive before it can feed to mature its gonads.

Three types of adults were used in survival experiments, namely: a) adult beetles, of uncertain age, allowed to feed on a piece of rotten meat 24 hrs before experiments; b) callow adults, used immediately on emergence, and not fed before experiments; c) overwintered adults, used immediately on emergence and not fed before experiments.

(1) Survival without food

Without a feed, beetles emerging from pupation or diapause survived from 5 - 7 days (Table 4:24). Not surprisingly, adults fed 24 hrs before experiments, survived much longer than this. The results from this study are similar to those of Springett (1967) who showed that callow N.humator survived about 5 days without food. Clearly burying beetles must feed soon after emergence from the soil if they are to survive, even without the need to mature gonads. Beetles with depleted fat reserves die fairly quickly if they do not feed. In the field, survival time may be even less than demonstrated here, as beetles will become progressively weaker as muscle breakdown occurs, and will become unable to find food or escape from predators.

About half the weight loss occurs in the first four days in adults fed 24 hrs before experiments (fig. 4:21). Weight loss is expressed as log $\frac{w_1}{w_2}$, where w_1 = original weight and w_2 = weight each subsequent day. The points are the means of all weights recorded, and standard deviation is shown. Day 0 is the day of feeding. Adults were weighed immediately after feeding and day 1 is the first day experimental weights were recorded. The curve was fitted by eye. The maximum weight lost is 25% of original body weight, occurring on average at day 20.

Table 4:24.

Survival of Necrophorus left in incubators at 15°C

Survival without food

	number of beetles	number of days surviving $\bar{x}$	SD
N.vespilloides			
callow adults on emergence	62	5.113	2.921
overwintered adult on emergence	25	6.530	1.716
adult after feeding	53	16.78	6.947
N.investigator			
overwintered/callow adult on emergence	18	7.259	4.228
adult after feeding	48	18.21	8.652

Survival when allowed to feed once on a conspecific

	Number of beetles	Number of days surviving $\bar{x}$	SD
N.vespilloides			
adult after feeding	41	27.64	5.201
callow adult	38	12.25	3.641
overwintered adult	19	14.68	5.220
N.investigator			
adult after feeding	37	26.44	3.829
overwintered/callow adult	16	15.51	4.332

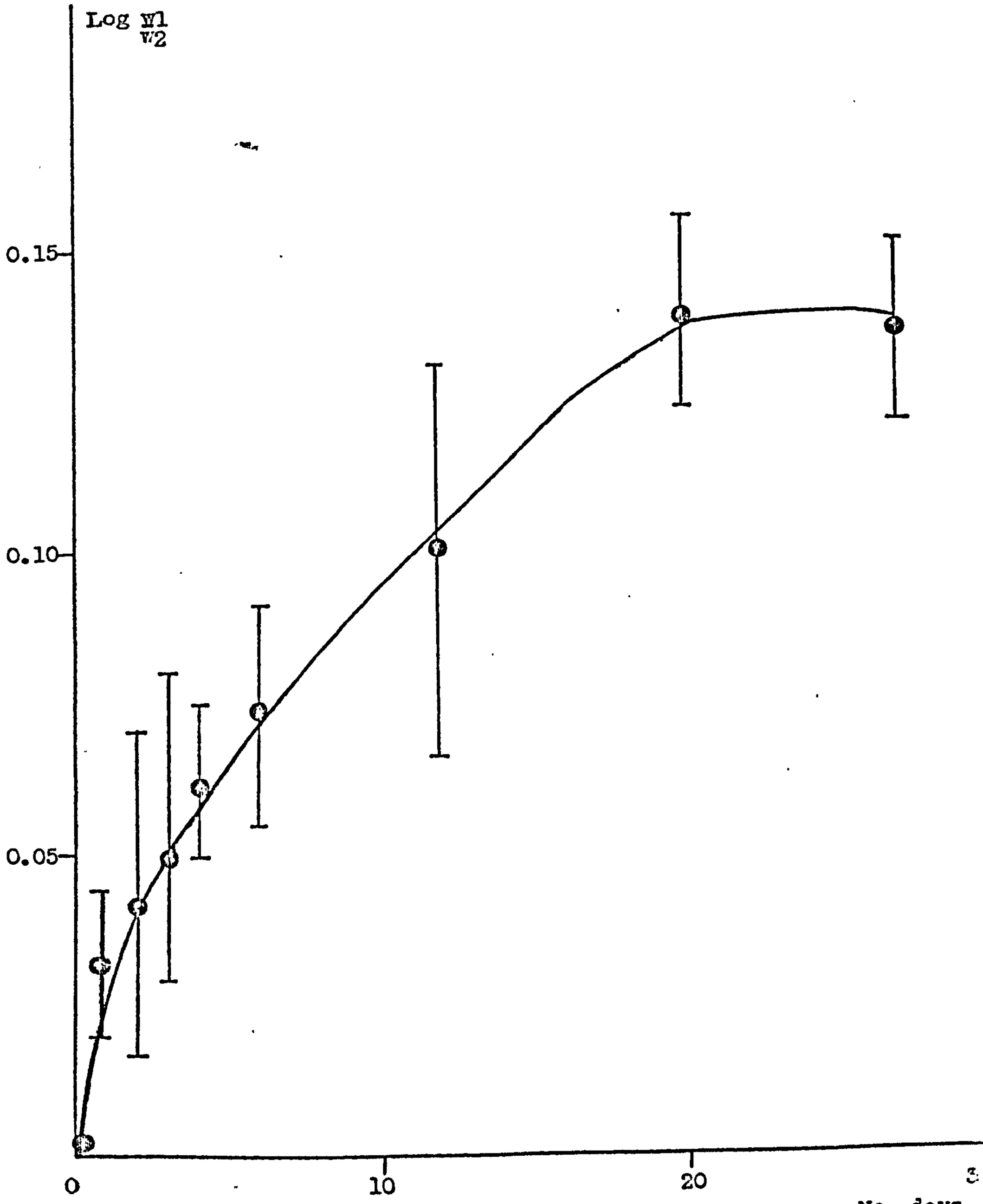
Fig. 4:21

Loss of weight by adult Necrophorus vespilloides

fed 24 hrs before first weighing.

● = mean weight loss

I = standard deviation


Log W1
W2
0.15
0.10
0.05
0
10
20
No. days
since fee

For adults fed 24 hrs before experiments, deaths started to occur at day 10, and all beetles were dead before day 34. Death occurred at weight losses varying from 5% of original body weight to 40%. Beetles dying at an early age lost a smaller proportion of body weight than those surviving longer, to be expected from fig. 4:21. Variation in the size of the beetles fat reserves may be responsible for the apparent variations in sensitivity to weight loss, and may explain why some beetles lost only a small proportion of their original body weight before dying (low fat reserves), while others could lose higher proportions of body weight and yet survive (large fat reserves). Unfed callow adults, or unfed overwintered adult beetles may have low fat reserves, and so starvation will soon lead to muscle breakdown and death, in these experiments before day 10.

(11) Survival and weight changes with food other than carrion.

The ability to find food is important for the survival of adult burying beetles, newly emerged from diapause or pupation (Table 4:24). Experiments were undertaken to test if Necrophorus would eat food other than carrion, and if so, how this affected survival.

a) Readiness to take food other than carrion

Burying beetles readily took food other than carrion, but not all types were eaten (Table 4:25). Adult Geotrupes, lycosid spiders, carabid and staphylinid beetles were not eaten, probably because they moved too quickly for burying beetles to catch. Adult Necrophorus were not eaten immediately, but when two adults were kept together without other food, one was ultimately eaten in every case. The other types of food offered were readily eaten. All unfed callow adults and unfed overwintered adults, and 65% of adults fed 24 hrs before experiments took food other than carrion the first time it was offered. There is a positive correlation between the number of times fed and the amount of

Table 4:25

Use of food other than carrion by Necrophorus

(With the exception of mealworms, all animals were collected from Inchcailloch, Rossdhu or the Ross Point. All are therefore potentially available to Necrophorus in the field)

Eaten by Necrophorus over a 24 hr. period	Not eaten by Necrophorus over a 24hr period
Tenebrio molitor L. (larvae) (mealworm)	Philonthus sp. (adult/larvae) (Staphylinidae)
Erannis defoliaria Clerck (larvae) (mottled umber moth)	Carabus violaceus L. (adult) (Carabidae)
Operophtera fagata Scharf (larvae) northern winter moth)	Pterostichus madidus F. (adult) (Carabidae)
Tortrix viridana L. (larvae) (green tortrix moth)	Abax sp. (adult) (Carabidae)
Calliphora sp (larvae) (blowfly)	Lycosa spp.
Lumbricus spp. (<6cm)* (earthworm)	Lumbricus spp. (>6cm)*
Necrophorus (adult)**	Geotrupes sylvaticus (adult) (Geotrupidae)
Necrophorus (pupae)	
Necrophorus (larvae)	

* The division in size is arbitrary. Large earthworms were attacked and damaged. Small earthworms were eaten completely.

** Adult Necrophorus were not necessarily eaten within 24 hrs. but if two adults were left together without food, one was invariably eaten.

food eaten ($r = 0.423$, d.of f. 22, $p < 0.05$) suggesting that the same beetles may become more ready to take food other than carrion the more often it is offered.

Potentially, therefore, burying beetles could use food other than carrion in the field. Observations of the beetles feeding behaviour suggest that prey is not actively pursued. Beetles bite at anything they touch. Animals are attacked only if the beetles jaws pierce the cuticle, hence the preference for soft bodied, slow moving animals (Table 4:25). Starved beetles continually open and close the mandibles, which may increase the chances of biting into suitable prey. Attacks cease if the prey wriggles free of the beetle jaws, and the beetles do not pursue the prey, but wander round until accidental contact is made once again.

b) Survival with food other than carrion.

When two burying beetles were kept in a container with no other food, one beetle was inevitably eaten. As a result of this single feed, the survivor lived longer than unfed beetles (Table 4:24). Similar observations were made using food other than carrion. Feeding once a week on mealworms not only prolonged survival indefinitely, but allowed beetles to maintain their body weights (fig. 4:22), despite fluctuations in weight between feeds, Adults fed 24 hrs before experiments lost 18.38%of body weight between feeds, and overwintered adults lost 15.70%. The expected weight loss over this time period is about 15% (fig. 4:21). All unfed control adults were dead by day 27, or day 11 (overwintered adults).

When beetles were given surplus food, their weight increased rapidly over the first week, then more slowly throughout the rest of the experiment (fig. 4:23). Therefore in the laboratory, feeding on material

Fig. 4:22

Weight changes of adult Necrophorus fed to repletion once per week

——— = Experimental adults fed once per week

— — — = control adults, unfed

* = all control adults dead

F = beetles fed

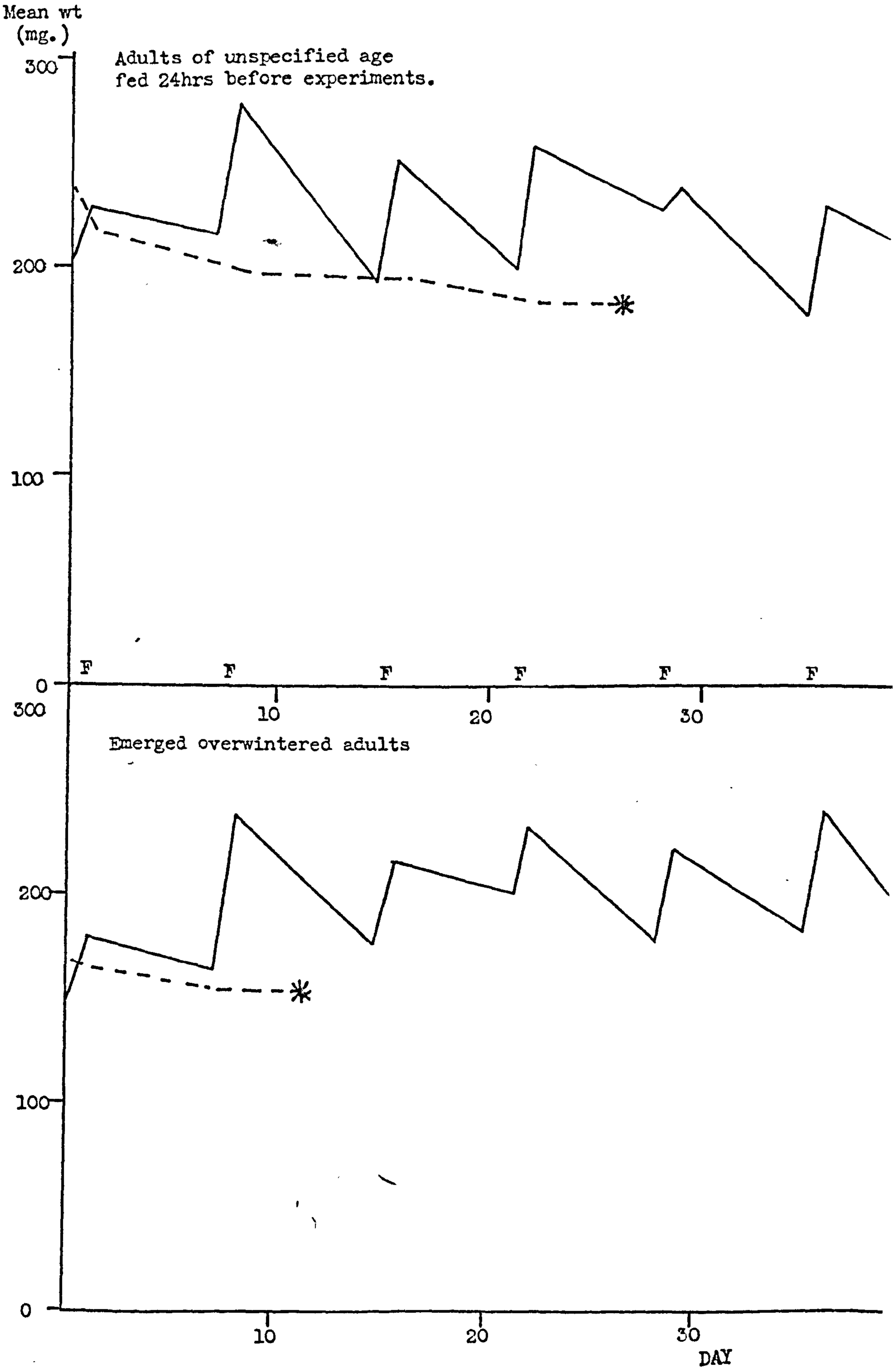
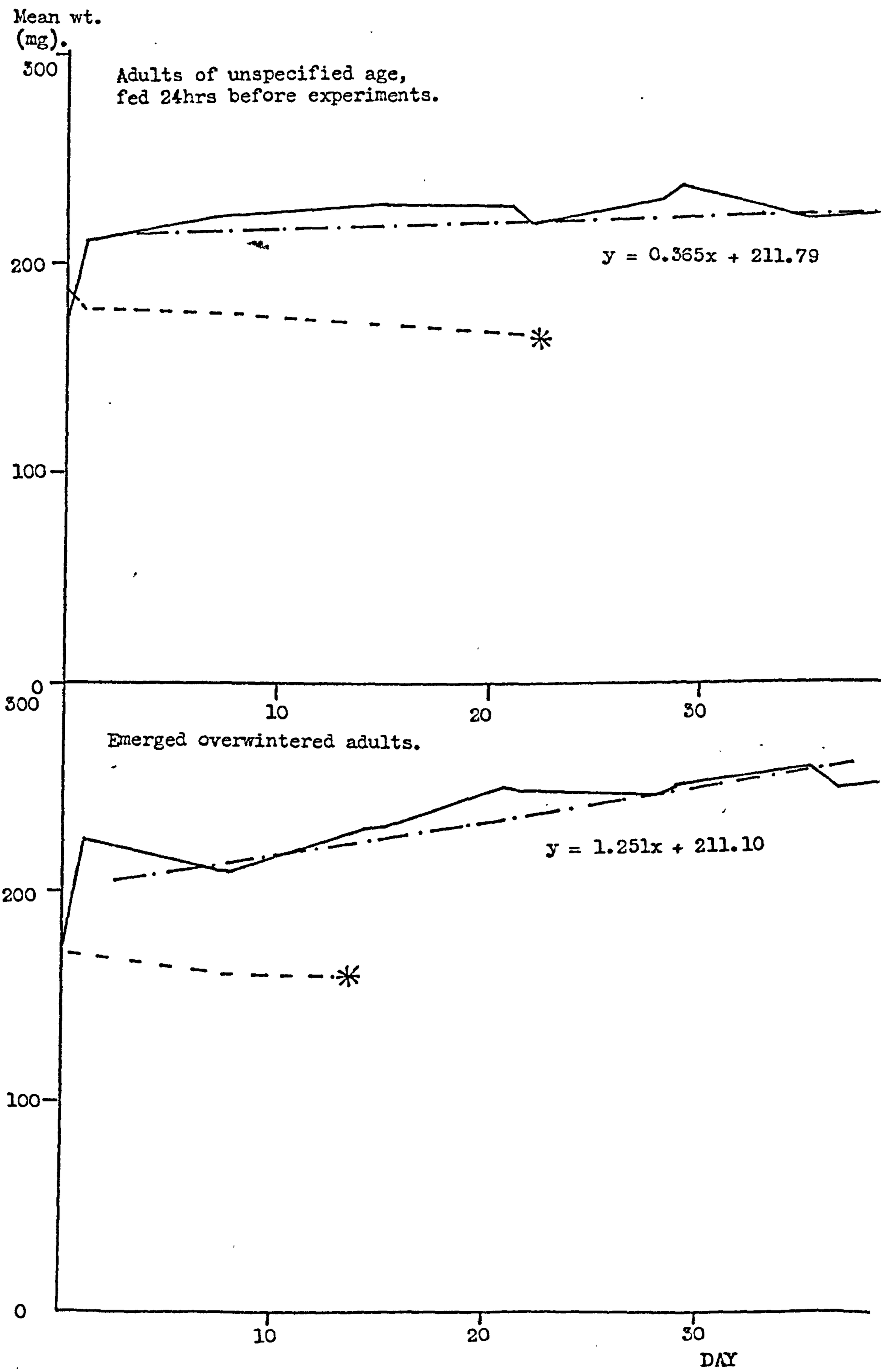

Mean wt
(mg.)
300
200
100
0
Adults of unspecified age
fed 24hrs before experiments.
F
F
F
F
F
F
0
10
20
30
300
Emerged overwintered adults
200
100
0
10
20
30
DAY

Fig. 4:23

Weight changes of adult Necrophorus kept with surplus food

——— = experimental adults with surplus food

Remaining symbols as for fig. 4:22


Mean wt.
(mg).
300
200
100
0
Adults of unspecified age,
fed 24hrs before experiments.
y = 0.365x + 211.79
10
20
30
Emerged overwintered adults.
y = 1.251x + 211.10
DAY

other than carrion can not only prolong survival and maintain body weight, but also lead to weight increase. This implies that there is food surplus to that required for survival. Such a surplus could presumably be used for maturation of gonads. The laboratory evidence suggests therefore that food other than carrion could be important for survival and maturation of gonads in the field.

4.3.2.2. Feeding prior to diapause.

N.vespilloides and N.humator emerging from pupation have little fat, e.g. on Inchcailloch it was always less than 3 (c.f. Table 2:9). Such adults must feed within about a week if they are to survive (Table 4:24). In addition, these beetles must store fat for diapause, and fig. 2:26 shows that the size of the fat body of immature adults can increase during this period. It was pointed out in 2.4 that the size of fat reserves varied with beetle density. It is possible that the effect of intraspecific competition on the amount of food consumed might affect the size of the fat body laid down. This could affect overwintering mortality.

During August and September, N.vespilloides and N.humator were occasionally observed feeding on corpses, making no attempt to bury them. Both species were often found on the same corpse (Table 4:26). Putman (1973) recorded similar behaviour in Wytham Wood, Oxford. These beetles were possibly immature, and feeding to lay down fat before going into diapause. What the beetles feed on during this period was not recorded, although Putman (1978) believed they were feeding on blowfly larvae.

As an introduction to feeding prior to diapause and its effects, a preliminary laboratory investigation was carried out on the effects on survival of varying the number of beetles feeding on a corpse. As few

Table 4:26

Number of N.vespilloides and N.humator found on corpses after mid August

Date (1974)	Type of corpse	Corpse Wt. (gms)	Number of beetles N. vespilloides	N. humator	Total
18 August	rat	322.4	2	5	7
21 "	mouse	21.6	2	0	2
27 "	mouse	16.4	1	2	3
27 "	mouse	22.2	3	1	4
27 "	rat	209.6	6	3	9
15 September	rat	143.4	5	1	6
18 "	chick	38.0	1	1	2
20 "	mouse	23.6	2	0	2
20 "	chick	42.1	2	0	2
20 "	supermouse	62.2	1	0	0
22 "	rat	186.4	4	2	6

beetles were available, the experiment was carried out only once, during the winter of 1974-75. N.vespilloides were kept at densities of 1, 3, 5, 7, 10 and 15 beetles on a mouse corpse in an experimental tray. The number of adults surviving the winter was counted. Five replicates of each density were used, the results for each density being combined for analysis (fig. 4:24). Although numbers are too small to draw conclusions, the resulting curve resembles the relationship between larval mortality and density, with an increase in mortality above a threshold (N_c). It is not known what caused the overwintering mortality in this experiment although starvation might be involved. The results suggest that beetle density and the amount of food available could have an effect on overwinter mortality.

4.4. Discussion

The variability of the clutch size in burying beetles is well known (Table 4:27) but has not yet been explained. Variation in the number of eggs in mature females, as observed in this study (Table 2:8) suggests that a factor operating prior to or during the development of the eggs may affect the size of the clutch. Springett (1967) suggests that the amount of feeding prior to egg development has an effect on the number of eggs matured. Experiments to test this hypothesis in this study were inconclusive, although there is some supporting circumstantial evidence. Feeding studies indicate that variation in the amount of food eaten by freshly emerged burying beetles can cause changes in body weight, surplus food leading to an increase in weight, restrictions in food leading to a loss in weight. An increase in body weight implies that there has been food surplus to that required for survival, enabling the beetle to increase its fat reserves or develop eggs. Therefore changes

Fig. 4:24

Relationship between adult density and overwintering mortality in Necrophorus vespilloides

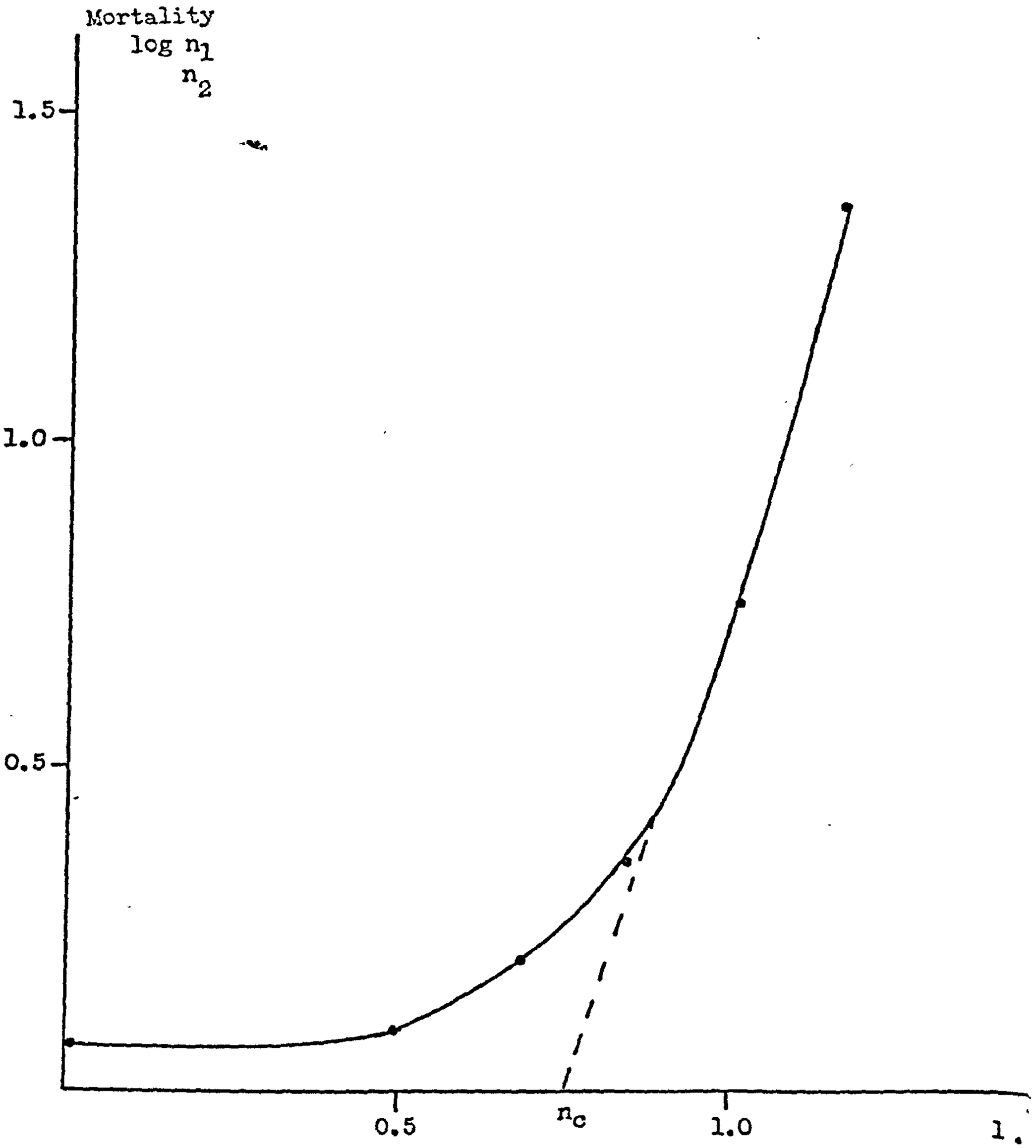

Mortality
log n_1
n_2
1.5
1.0
0.5
0.5
n_c
1.0
1.
Log no adults
/ corpse

Table 4:27

Variation in numbers of eggs laid by Necrophorus

Species	mean number of eggs	Variation	Author
N.vespillo	14.25±6.88	4 - 24	Pukowski (1933)
N.vespillo	15.00	10 - 24	Roussel (1964a)
N.fossor (=N.interruptus)	24	-	Roussel (1964b)
N.humator	12.5±4.2	3 - 24	Springett (1967)
N.investigator	11.1±6.8	3 - 24	

in the amount of food eaten could cause changes in the amount available for production of eggs, thereby affecting clutch size.

The egg production of several other insects is known to be affected by the quality or availability of food. Protein deficient diets affect the ovaries of the blowfly Phormia regina (Orr, 1964a, b; Bennettová-Režábová, 1972; Stoffolano, 1977), and food quality affects the number of eggs matured by female face flies, Musca vetustissima (Hughes and Walker, 1970). Protein feeding is a requirement for successful egg development in Calliphora erythrocephala (Strangeways-Dixon, 1961), Phormia regina (Dethier, 1961) and Musca vetustissima (Miller and Treece, 1968; Hughes, 1974) and can be shown to be cyclic in relation to the development of successive batches of eggs. The relationship between the blood meal and fecundity in blood sucking diptera, such as the tsetse fly, Glossina spp., has been well studied (e.g. Denlinger and Ma, 1974). Necrophorus will resemble these insects if clutch size is affected by the amount of food available during egg development.

It is not known for certain what burying beetles feed on while maturing their eggs. Although Necrophorus are widely believed to be carrion feeders (Fabre, 1919), many observations suggest that they may in fact be predators, usually feeding on dipterous larvae on or near corpses (Clark, 1895; Steele, 1927; Pukowski, 1933; Fichter, 1949; Elton, 1966, Springett, 1967; Putman, 1978). Elton (1966) describes N.vespilloides pursuing dipterous larvae in decomposing fungi. This behaviour may explain the records of burying beetles trapped in flowers and fungi (Hofmann, 1902). As well as feeding on dipterous larvae near carcasses, N.germanicus attacks and eats adult Geotrupes (Hofmann, 1902; Pukowski, 1933). Cannibalism has also been observed (Roussel, 1964a, b;

this study). Similar feeding habits have been recorded for other carrion inhabiting silphids, e.g. Necrodes littoralis has been observed to prey on molluscs (Marikovskiy, 1974), and Silpha obscura feeds on dipterous larvae in dead snails (Beaver, 1977). Some species of silphid beetle are well known as predators, e.g. Phosphuga atrata (R. Dobson, pers. comm.), Silpha carinata (Sandhall, 1974) while others are believed to be, e.g. S.ramosa (Brewer and Bacon, 1975). Burying beetles may, therefore, obtain much of their food by predation. Laboratory studies show that burying beetles will eat any animal they can catch, for example blowfly larvae, caterpillars, small earthworms. Variation in the availability of these animals during development of the eggs may be responsible for variations in clutch size of Necrophorus. Confirmation of this hypothesis must await further studies on relationships between burying beetles and their prey.

There is a second course of variation in clutch size, which takes effect between maturation of eggs and oviposition. This seems to be influenced by corpse size. On corpses less than 10gms in weight, fewer eggs are laid by N.vespilloides than are matured, while on corpses greater than 10gms, the number of eggs laid is the same as the number matured. Similarly N.investigator lays fewer eggs on mice than are matured while on rats all the mature eggs are laid. In the few cases where N.humator buries mice, fewer eggs are laid than are matured. The presence of mature eggs in post reproductive females is further evidence that, in some cases, eggs are retained by the female and not laid. These results suggest that burying beetles can vary the number of eggs they lay, depending on corpse size. The implication of this is that the corpses on which fewer eggs are laid are 'less suitable' for breeding than those on which all mature eggs are laid. The retention of eggs may be seen as a response by the beetle to avoid wasting reproductive effort on a corpse

which is not suitable. If burying beetles breed more than once, which may or may not occur, females may retain eggs in order to spare themselves from looking after larvae which will not develop, thereby conserving themselves for breeding again. Eggs may be retained in the expectation of finding another corpse. Until it can be shown that Necrophorus breeds more than once, this hypothesis must remain speculative.

Experimental manipulation of clutch size does suggest an explanation for reduction in clutch size on smaller corpses. When clutches are increased in size artificially, mortality remains at normal levels, and is independent of density up to a particular clutch size - the threshold density. Above threshold density, mortality is density dependent, of the scramble type (Nicholson, 1954; Hassell, 1975) and resembles that observed in other populations of insects that live in a temporary food source, such as blowfly (Nicholson, 1954) and Drosophila larvae (Millar, 1964). Mortality above threshold may be due to starvation, as corresponding changes in larval weight are observed. Threshold density varies with corpse size, becoming lower on smaller corpses. The number of eggs actually laid by burying beetles is always less than the (artificial) threshold density. Reduction in clutch size may, therefore, be interpreted as a method of preventing density dependent mortality on corpses when threshold density is less than the number of eggs matured. As density dependent mortality may occur on smaller corpses if all the eggs were laid, the observed number of eggs is actually the most productive clutch size, even when less than the total number of eggs matured. Burying beetles may resemble many birds (e.g. Perrins and Moss, 1975) in having a most productive clutch size associated with the carrying capacity of the environment.

Variability in the number of eggs laid, or fecundity, has been observed in many insects. In most cases, variation in fecundity is

caused by events during the development of the insect. For example larval competition for food affects adult size, which in turn affects fecundity in Sarcophaga (Beaver, 1977). This has also been observed in bark beetles, reduced adult size being due to larval competition for food in Scolytus scolytus, S.multistratus and Tornicus piniperda (Beaver, 1974); smaller females have a lower fecundity than larger, and lay only a small fraction of the eggs they are capable of producing in Ips typographicus (Thalenhorst, 1953), Dendroctonus morticolae (Reid, 1962) and D.ponderosae (McGehey, 1971). A similar relationship between larval competition and adult size has been observed in Ephestia kuhnellia, Lepidoptera (Ullyett and van der Merwe, 1947), E.cautella, Lepidoptera (Takahashi, 1956), Phodia interpunctella, Lepidoptera (Snyman, 1949) Lucilia cuprina, Diptera (Nicholson, 1954), Drosophila melanogaster and D.simulans, Diptera (Miller, 1964) and Anagasta kuhnellia, Lepidoptera (Hassell and Huffaker, 1969). There are fewer examples of a reduction in the number of eggs as a response to factors operating at the time of oviposition, as occurs in Necrophorus. Such a response has been demonstrated in the large copper butterfly (Lycaena dispar), by Duffey (1968, 1977). In this species, females can potentially lay 300-600 eggs. The number of eggs actually laid is usually less than this, and varies with external factors at the time of oviposition, such as air temperatures and size of host plant. The fecundity of aphids is often affected by the number of surrounding individuals (e.g. Dixon, 1973). Therefore, the reduction in number of eggs laid by burying beetles as a response to unsuitable corpses is not unique, but is certainly a subtle reaction to changes in the environment.

The hypothesis that some corpses will support fewer larvae than others may help to explain the corpse preferences shown by burying beetles, and discussed earlier. N.vespilloides shows no preference for

corpses greater than 10gms in size, and in these corpses the threshold density is greater than the normal clutch size. N.investigator may prefer rats to mice. Mouse corpses cause a reduction in clutch size in this species, whereas on rats the full number of eggs is laid. N.humator may prefer larger corpses, and must reduce the number of eggs laid if small corpses are buried. Corpse selection may be interpreted as a behavioural response to maximise the number of young that can be raised. If this is the case, a number of questions arise about the behavioural aspects of corpse selection and burial. For example, how does the beetle assess the size and suitability of the corpse for breeding? This may be one of the functions of the behaviour noted by Fabre (1919) and all other students of Necrophorus, namely the beetles crawling over the carcass and lifting the corpse up. These may have other functions, such as finding blowfly eggs (Springett, 1967) or testing mobility (Milne and Milne, 1976), but may well also assess the size of the corpse and its ease of displacement (Pukowski, 1933) or weight and centre of gravity (Niemitz, 1972). If a corpse is assessed as unsuitable what does the beetle do then? Does it bury the corpse, lay a reduced number of eggs and perhaps try to breed again in order to lay the rest of its eggs? Or does it abandon the corpse in order to find a more suitable carcass elsewhere? Many factors may be involved, such as the age and condition of the beetle, the number of times it has been driven from a corpse by other beetles, number of unsuitable corpses already encountered and so on. Hughes and Walker (1970), for example, show that newly gravid female face flies will not lay eggs on dung of poor quality, while older flies may do so. Answers to this question must remain speculative until the behavioural aspects of relationships between burying beetles and the corpse have been studied.

In section 3.4 it was suggested that the corpses on Inchcailloch

might be less suitable for N.investigator than for N.vespilloides. This hypothesis is supported when the size of corpse found on Inchcailloch is examined with regard to the number of larvae that each will support. This assumes that the results obtained from mice and rats are applicable to other corpses. The majority of corpses on Inchcailloch (adult shrews, juvenile and adult voles) are likely to weigh 10 - 30gms. On these, N.vespilloides will be able to lay all its eggs. Only on juvenile shrews (7gms) will the clutch size of N.vespilloides be reduced. None of these corpses will allow N.investigator to lay all its eggs, and so this species will lay fewer eggs than it could on rat sized corpses. The reproductivity of N.investigator on Inchcailloch in terms of number of larvae matured, will be less than that of N.vespilloides. Not only are fewer corpses potentially available to N.investigator, but fewer larvae are reared on the corpses that are available. Retention of eggs in post reproductive females (Table 2:8) suggests that neither species is, in fact, breeding to its full capacity on Inchcailloch.

The relationship between corpse size and number of eggs laid on corpses weighing less than 10gms has been barely touched on in this study. This topic could be further investigated by normal feeding and transplant experiments using baby mice. These experiments would decide whether clutch size and threshold density decrease in parallel on small corpses.

SECTION 5.

FACTORS AFFECTING NECROPHORUS POPULATION NUMBERS

5. FACTORS AFFECTING NECROPHORUS POPULATION NUMBERS

5.1. Introduction

Two types of factor may affect burying beetle populations, those causing fluctuations, and those leading to regulation. The terms 'fluctuation' and 'regulation' are often confused. In this study, a fluctuation will be regarded as the observed effect on the population of any disturbing factor, whereas regulation will be regarded as the effect of a stabilising factor on a population. 'Any type of numerical variation in a population, whether or not a mathematically detectable consistency or trend can be discerned' (McFadyen, 1963) will be considered a fluctuation. Changes in environmental factors, such as the weather, or in food supply, predation or parasitism may lead to fluctuations (Solomon, 1969), and in species with seasonal reproduction, short term fluctuations will occur each year due to the influx of young. Factors reducing the effects of fluctuations on populations are possible regulatory factors. It has been argued (Klomp, 1962) that regulation of population numbers must be due to density dependent processes, which can lead to stable equilibria, and also to cyclic or irregular oscillations (Hassell, Lawton and May, 1976). Density dependent processes can be due to inter or intra-specific interactions, such as intraspecific competition for food, space, cover or oviposition sites, and interactions with predators, parasites and pathogens (Klomp, 1964). These may act on adults, eggs or larvae. Density dependent regulatory processes have been shown to act in a wide variety of species (e.g. Podoler and Rogers, 1975; Stubbs, 1977).

Observations made in this study show that fluctuations do occur in burying beetle populations. The pattern of fluctuation differs, depending on the life cycle of the beetle concerned. Regular, short term fluctuations in numbers of N.vespilloides take place between spring

and autumn (figs. 2:10, 2:12), due to the influx of young into the population. The extent of the fluctuation varied from year to year, being highest in 1975 and lowest in 1974. Despite these variations in the number of overwintering adults each autumn, the number of animals trapped in spring was similar in the three years of the study. Smaller fluctuations were observed in the population of N.investigator, which were highest in 1973 and lowest in 1974. Similar fluctuations in an N.investigator population were observed by Springett (1967).

Fluctuations in the numbers of burying beetles were explained by Springett(1967) who considered that the major factor regulating Necrophorus populations is availability of suitable corpses, leading to density dependent competition for corpses. As a result, fluctuation in Necrophorus numbers are caused by variation in the number of corpses. This author also suggested that the availability of food for gonad maturation, and the ability of burying beetles to destroy their competitors, fly larvae, might affect the numbers of Necrophorus able to breed, and that a major, as yet undiscovered parasite might depress population numbers. Novák (1965b) suggested that fluctuations were caused by removal of competing species during experiments. Neither of these hypothesis was considered entirely satisfactory to explain the fluctuations observed in this study. Therefore, experimental and population data were examined in order to identify these factors which cause burying beetle populations to increase and decrease. The results of the study are insufficient to prove that particular factors influence populations, but do indicate some factors which may be involved.

5.2. Possible factors affecting Burying Beetle Populations

Many factors may, potentially, influence the size of Necrophorus populations (figs. 5.:1, 5:2). In this section, particular attention will

Fig. 5:1

Factors potentially influencing population numbers of N.vespilloides

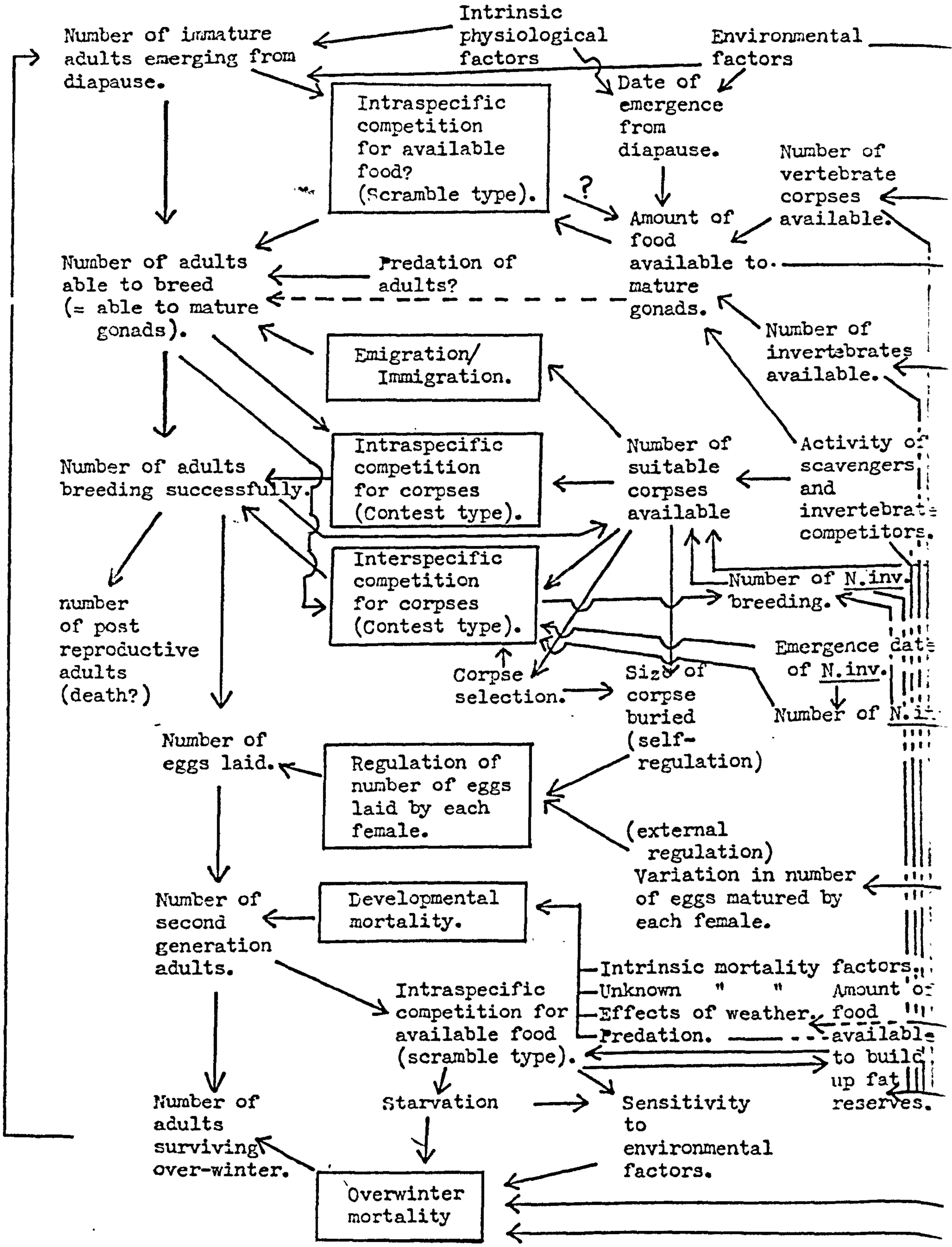
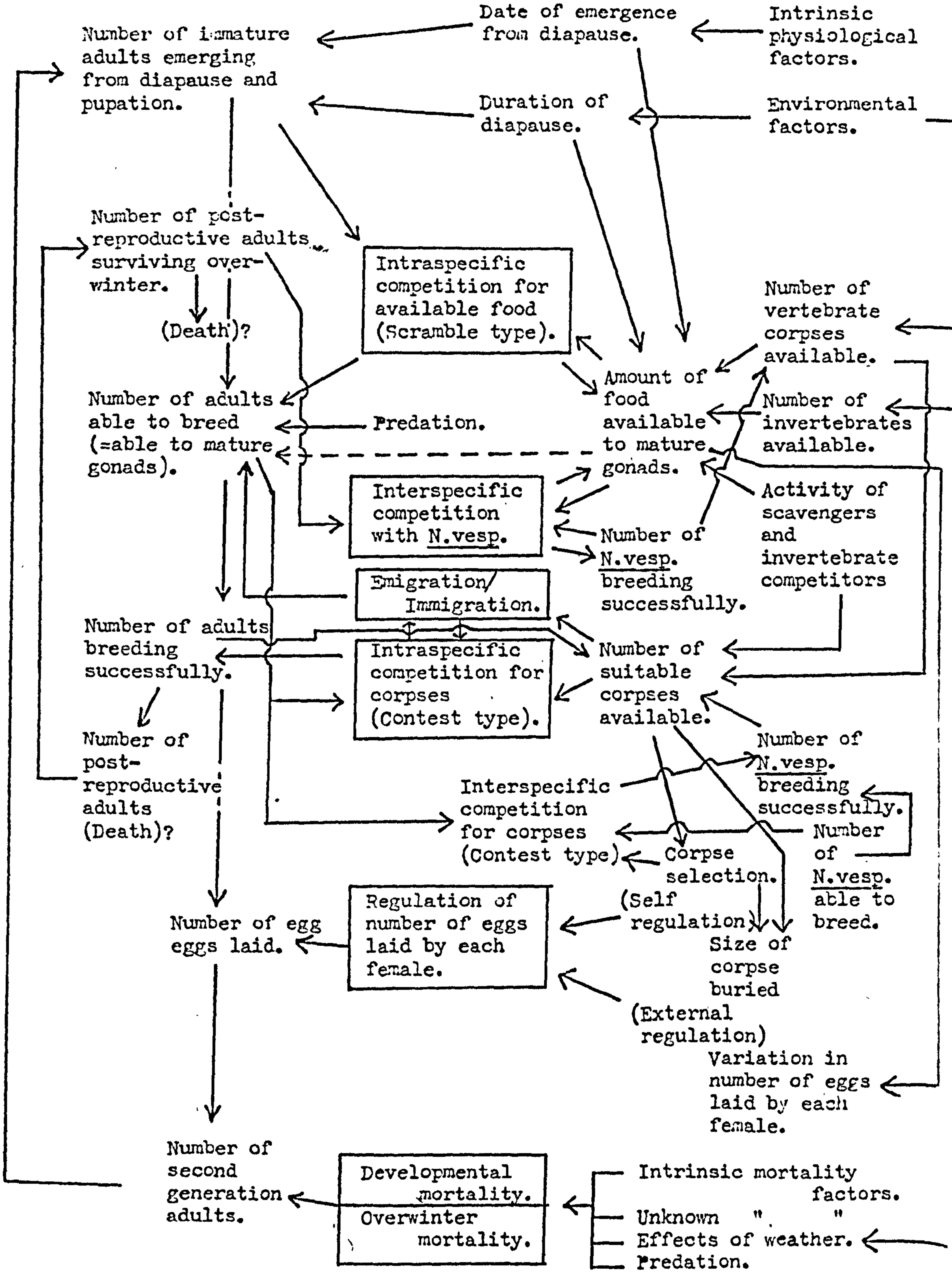

Intrinsic physiological factors
Environmental factors
Number of immature adults emerging from diapause.
Intraspecific competition for available food? (Scramble type).
Date of emergence from diapause.
Number of vertebrate corpses available.
?
Amount of food available to mature gonads.
Number of adults able to breed (= able to mature gonads).
Predation of adults?
Number of invertebrates available.
Emigration/ Immigration.
Intraspecific competition for corpses (Contest type).
Number of suitable corpses available
Activity of scavengers and invertebrate competitors.
Number of adults breeding successfully.
Interspecific competition for corpses (Contest type).
Number of N.inv. breeding.
number of post reproductive adults (death?)
Corpse selection.
Size of corpse buried (self-regulation)
Emergence date of N.inv.
Number of N.i
Number of eggs laid.
Regulation of number of eggs laid by each female.
(external regulation)
Variation in number of eggs matured by each female.
Number of second generation adults.
Developmental mortality.
Intrinsic mortality factors.
Unknown " "
Effects of weather.
Predation.
Amount of food available to build up fat reserves.
Intraspecific competition for available food (scramble type).
Starvation
Sensitivity to environmental factors.
Number of adults surviving over-winter.
Overwinter mortality
= Potential regulatory factors.

Fig. 5:2

Factors potentially influencing population numbers

of N.investigator


Number of immature adults emerging from diapause and pupation.
Date of emergence from diapause.
Intrinsic physiological factors.
Duration of diapause.
Environmental factors.
Number of post-reproductive adults surviving over-winter.
(Death)?
Intraspecific competition for available food (Scramble type).
Number of vertebrate corpses available.
Number of adults able to breed (=able to mature gonads).
Predation.
Amount of food available to mature gonads.
Number of invertebrates available.
Interspecific competition with N.vesp.
Number of N.vesp. breeding successfully.
Activity of scavengers and invertebrate competitors
Emigration/ Immigration.
Number of adults breeding successfully.
Intraspecific competition for corpses (Contest type).
Number of suitable corpses available.
Number of post-reproductive adults (Death)?
Number of N.vesp. breeding successfully.
Interspecific competition for corpses (Contest type)
Corpse selection.
Number of N.vesp. able to breed.
Regulation of number of eggs laid by each female.
Number of egg eggs laid.
(Self regulation)
Size of corpse buried
(External regulation)
Variation in number of eggs laid by each female.
Number of second generation adults.
Developmental mortality.
Overwinter mortality.
Intrinsic mortality factors.
Unknown " "
Effects of weather.
Predation.

be paid to those causing:

1) Variation in the size of the late summer peak of N.vespilloides from year to year.

2) Variation in the size of the N.investigator population from year to year.

3) Maintenance of size of spring peak of N.vespilloides at similar levels from year to year.

(1) Variation in the size of the late summer peak of N.vespilloides from year to year.

This is due almost entirely to variations in the number of offspring produced by breeding adults. Although the population may contain other types of individual during this period, i.e. first generation immature, mature and post reproductive adults (figs. 2:19 - 2:21), the bulk of the population will consist of second generation adults.

Factors which may influence the number of offspring produced by breeding adults are summarised in Table 5:1. All of these factors may vary thereby causing variation in the number of offspring produced by breeding adults.

The factor most likely to vary from year to year, and sufficient to cause the observed variation in number of second generation adults is the number of adults actually breeding. If the number of breeding adults is assumed to be normally in excess of the number of corpses, leading to intraspecific competition (Springett, 1967), the number of corpses available for breeding may be regarded as a major factor influencing the number of offspring produced by breeding adults. Variation in the number of corpses available from year to year could lead to the observed variation in the number of second generation adults. Circumstantial

Table 5:1

Factors influencing number of offspring produced by breeding adult burying beetles.

Number of 2nd generation adults		Causes of variation	
		Known	Possible
	Developmental mortality	Not affected by clutch size in normal clutches	Predation environmental factors Larval starvation
	Number of eggs laid	Number of eggs matured	Availability of food during and before egg development
		size of corpse buried	Carrying capacity of corpse in terms of larval survival
	Number of adults breeding	Number of corpses available	Environmental factors; size of vertebrate population: activity of scavengers and invertebrate competition, includin other *Necrophorus* spp.
		Number of beetles in breeding condition (always in excess of corpse supply?)	Number of adults emerging from diapause; food available during development of gonads; predation; immigration and emigration

evidence from the field may support this hypothesis. The lowest number of second generation adults was produced in 1974. The period April to June 1974 was the warmest and driest of the three years studied. It is known that cold wet weather can cause vertebrate mortality, particularly among juvenile stages. The weather conditions of 1974 could conceivably have allowed good vertebrate survival and consequently poor breeding for N.vespilloides.

(2) Variation in size of N.investigator populations from year to year.

The population of N.investigator that is observed each year consists mainly of the offspring of that which bred the previous year, with a few post reproductive individuals of the previous generation (figs. 2:22 - 2:24). The population is, therefore, analagous to that of N.vespilloides in late summer, as discussed previously and similar factors will influence the population (Table 5:1). The major factor affecting the size of the population may be the number of corpses available for breeding in the previous year. This is the method proposed by Springett (1967), whereby the size of N.investigator populations is controlled.

Although the size of late summer N.vespilloides and N.investigator populations may be controlled by similar factors, the extent of the fluctuations differs greatly between the two species. This may be due to several factors which influence N.investigator differently from N.vespilloides (Table 5:2). The population of N.investigator on Inchcailloch is smaller than that of N.vespilloides because N.investigator seems to produce fewer offspring, due to the number and type of carrion found there. As a result, the populations of N.investigator fluctuate at a lower level.

Table 5:2.

Factors causing the population of N.investigator to fluctuate at a lower level than that of N.vespilloides.

Known	Possible
Fewer eggs matured by N.investigator	Fewer corpses available for N.investigator breeding on Inchcailloch.
Fewer eggs laid on small corpses by N.investigator	Corpses available are less suitable for breeding of N.investigator than for N.vespilloides.
Developmental mortality of N.investigator higher	
Consequently, fewer adults produced by N.investigator than by N.vespilloides.	

(3) Maintenance of the spring peak of N.vespilloides at similar levels from year to year.

The population of breeding N.vespilloides adults in the spring of each year consists of the same individuals that were present in the autumn of the previous year. Despite fluctuations in the latter, the spring peaks of each year are similar. The only factor separating the two is overwinter mortality. This must reduce the autumn population to the same level each year. Consideration of what is known (Table 5:3) leads to the hypothesis that intraspecific competition among immature adults for food prior to entering diapause may lead to density dependent mortality overwinter. Such a mortality could cause the observed variation in number of immature adults to be stabilised, as occurs in the field. Stabilisation of the numbers of breeding adults in this way could be considered population regulation.

It is not apparent how the N.investigator population could be regulated, as overwinter mortality in this species is not density dependent. The population of N.investigator might be expected to fluctuate from year to year, and indeed this appears to be the case. There is insufficient data to decide whether regulation occurs at any other stage in the life cycle of N.investigator.

5.3. Discussion

Springett (1967) believed that fluctuations in the numbers of burying beetles were due mainly to fluctuations in the numbers of corpses available for breeding. While this hypothesis is all that is required to explain fluctuations of species such as N.investigator, which overwinter as prepupae, it is inadequate to explain the fluctuation of species such as N.vespilloides, in which immature adults are produced in late summer, feed to build up fat reserves and spend the winter in

Table 5:3.

Factors affecting overwinter mortality of N.vespilloides

Known	Possible
Overwinter mortality occurs and in the laboratory may be density dependent.	Density dependent overwinter mortality reduces the autumn population to that observed in spring.
Fat reserves are required by overwintering adults.	Overwinter mortality is a result of competition for food to develop fat reserves.
In the field, fat reserves are low when the population is high, and high when the population is low.	The agents of mortality may be starvation or sensitivity to weather.

diapause. In these species, fluctuations in the number of immature adults may be caused by fluctuations in corpse supply, and may be reduced by a density dependent mortality occurring overwinter. This may be the result of intraspecific competition for food which occurs prior to diapause.

The size of the burying beetle population may bear no relation to the resources actually available for breeding, as the population size is decided the year before. The delayed response to resource availability is an unavoidable consequence of the burying beetle's yearly life cycle. This may seem to be very inefficient as far as breeding and use of resources is concerned, but this is not necessarily so. It is usually assumed (Springett, 1967) that a burying beetle population always contains more breeding adults than there are corpses available, and as a result there is always intraspecific competition for carrion. Therefore there are always enough individuals in the population to deal with the carrion available. The rest of the population is in excess of requirements. Any increase in corpse availability means more beetles will breed, while a decrease in corpse availability means a larger excess of population. Because there will be enough resources for only a part of the population, there is no need for a particularly close relationship between corpse availability and population size. Overproduction of young ensures that there are always enough individuals to exploit the resource. Due to the high survival of the larvae, each corpse that is buried will ensure the production of 6 - 9 adults. Therefore beetles that do breed will be able to maintain the overproduction from year to year, providing corpse supply does not vary too widely.

In the absence of data, further speculation is valueless. However, it appears that burying beetles may respond to the limited and

variable nature of the resources it uses by ensuring that there are always enough individuals to deal with the corpses that are available. A consequence of this is that there will always be excess individuals in the population which will be unable to breed. Therefore, in essence, burying beetle populations may be controlled entirely by the availability of carrion for breeding, excess individuals in the population being removed in different ways depending on the life cycle.

SECTION 6.

GENERAL DISCUSSION

6. GENERAL DISCUSSION

Before reproducing, a burying beetle must find a corpse and defend it against competitors. The beetle must also overcome the problems created by the nature of the corpse itself. Only if these obstacles are successfully overcome will the beetle be able to rear its young. That burying beetles are successful is seen by the absence of carrion from many areas, as a result of their activities. In this section, two particular aspects of the ecology of Necrophorus will be discussed, namely interspecific competition and the adaptations which enable burying beetles to breed successfully on carrion.

It is widely believed that when two species compete, one will displace the other. This has been shown mathematically (Volterra, 1926; Lotka, 1932; Gause, 1934) and by field and laboratory investigation (Park, 1948, 1954; Frank, 1957; Crombie, 1944, 1945; Birch, Park and Frank, 1951; Connel, 1961a, b; Brian, 1952; Pontin, 1961, 1963, 1969; Reynoldson and Lock, 1976). Species can coexist only when they do not occupy exactly the same niche (Hutchinson, 1957). Most species show differences in habitats and requirements, thereby avoiding competition. For example, Daphnia pulicaria and Simocephalus vetulus may occur in different microhabitats in a pond (Frank, 1952) while one of the reasons that Balanus balanoides and Cthalamus stellatus coexist is that they have different resistances to physical factors. Of the five coexisting species of warbler studied by MacArthur (1952), three had slightly different habitats from each other, one was an unspecified marginal species with a low population density and the fifth was restricted to one type of food, leaving the area when its food was not available. Brian (1952) showed that four species of ant could coexist because they occupied different types of nest site.

When two species overlap in their niche requirements, they may become potential competitors (Hutchinson, 1954). The degree of overlap in niche requirements will determine whether the species can coexist. For example the triclads Polycelis temuis, P.nigra, Dugesia polychroa and Dendrocoelum lacteum prey on the same food items, and can only coexist because each species has a food refuge (Reynoldson and Davies, 1970; Reynoldson and Bellamy, 1973; Reynoldson, 1975). Where there is no food refuge, one species is displaced by another (Lock and Reynoldson, 1970). Food refuge is a term coined by Reynoldson (1966) for that part of the diet in which a particular triclad species is competitively superior. Reynoldson and Davies (1970) suggest that if two or more species are to coexist without spatial or temporal separation, each species must have at least a 30% competitive superiority in one part of the general food resource.

As far as breeding is concerned, the three species of burying beetle found in the study area provide a good example of niche separation in closely-related and ecologically similar species, as well as some evidence of niche overlap. All three species are found in the same habitat, but N. humator avoids competition with the other two species by breeding mainly on large carcasses. Although N.vespilloides and N.investigator may prefer carrion of different sizes, corpse selection is unlikely to be possible in the study area. The two species will, therefore, utilise the same resource. Competition for corpses may be partly avoided because the two species have different life cycles. As a result, N.vespilloides and N.investigator require corpses for breeding at different times of the year. Breeding periods overlap in the study area however, and so this method of separation is not completely effective. There is a period when both species may be breeding and so in this area there may be some overlap of niches. As a result there is a potential

for interspecific competition during the overlap period. There is some circumstantial evidence that such competition may occur, although the data is subject to other interpretations. However, even if interspecific competition does occur, N.vespilloides and N.investigator appear to coexist, and may have done so for some time (Elliot, Laurie and Murdoch, 1901). These two species have also coexisted for a long time in other areas (e.g. Welch, 1973). They may be able to coexist because each species can bury corpses without interspecific competition over part of the breeding period - i.e. a breeding refuge (by analogy with the food refuge of Reynoldson, 1966). This is not the complete answer however. Experiments show that N.investigator is competitively superior to N.vespilloides and might be expected to displace N.vespilloides from the study area in time. That this has not occurred suggests that some factor must act on N.investigator to prevent this species emerging earlier in the year and thereby displacing N.vespilloides. This factor (or factors) was not identified during the study. It is possible that the disappearance of N.vespillo from the Loch Lomond area (Elliot, Laurie and Murdoch, 1901) and from Monks Wood, Huntingdon (Welch, 1973) was a consequence of a niche overlap between N.vespillo and N.vespilloides, which was not mitigated by some other factor. The nature of the relationship between N.vespilloides and N.investigator can only be determined by further experiment and long term study of the populations in the study area.

Two principal problems are associated with using carrion as a source of energy. Firstly, carrion is a temporary habitat (Elton, 1966; Southwood, 1977). Rapid changes occur during decomposition. These are often caused by the activities of organisms living in the corpse (Beaver, 1977). Carrion may be regarded as an unstable habitat because conditions may rapidly become unsuitable for a particular type of

organism. Secondly, carrion is a habitat for a variety of arthropods and microorganisms, all striving to use the limited amount of energy provided by a corpse (Beaver, 1977). As a result, competition within carrion may be intense. Carrion and the organisms associated with it have been widely studied, with particular emphasis on succession, e.g. in cats (Illingworth, 1927), sheep (Mackerras and Freney, 1933; Fuller, 1934; Macleod, 1943; Waterhouse, 1947), rabbits (Chapman and Sankey, 1955), dogs (Reed, 1953), pigs (Payne, 1965, 1967), rats (Millican, 1965), chickens (Wasti, 1972) and mice (Putman, 1973).

Necrophorus overcomes the problems of carrion in several ways (Table 6:1). By burying the corpse, Necrophorus removes its resource from the general carrion community and provides a unique source of food for its own larvae (Elton, 1966). Not only is competition thereby avoided, but a major source of the changes associated with decomposition, the arthropods, are removed. Stripping the fur and feathers from a corpse may also remove arthropods, particularly dipterous larvae, while micro-organisms may be inhibited by antibiotic substances in crop secretions (Springett, 1967). The symbiotic relationships developed between burying beetles and the mites Poecilochirus necrophori may be another adaptation to remove arthropods from the corpse, as the mites eat dipterous eggs (Springett, 1968). Carrion which has not been exposed to arthropods decomposes more slowly than that with normal arthropod succession (Wasti, 1972; Putman, 1977). Burial may slow down the decomposition of the corpse, making the habitat more stable for the development of Necrophorus larvae.

After burial, the female beetle remains with the corpse (Fabre, 1919; Pukowski, 1933; Springett, 1967; this study), repairing the walls of the crypt, defending the larvae against predators and feeding

Table 6:1.

The characteristics of carrion and the adaptations developed by burying beetles to overcome them.

Characteristic of carrion	Adaptation by burying beetle
Many competitors for a limited amount of energy.	Burial of a corpse as a unique source of food for the larvae. (aided by a symbiotic association with mites)
Rapid changes due to decomposition - caused mainly by activities of arthropods and microorganisms.	Decomposition slowed down by burial, removes corpse from arthropods.
Habitat temporary and unstable.	Removal of fur and secretion of antibiotics may remove arthropods and microorganisms.
	Protection, feeding and maintenance of larvae by females - creates stable conditions for larvae.
	Physical aspects of environment may be stabilised for larvae by the design of the crypt.

the early stages of each instar on regurgitated crop contents (Pukowski, 1933). If the female is removed at any time before the third instar, the larvae die (Springett, 1967). By caring for their larvae in this way, burying beetles show presocial behaviour (Wilson, 1971, 1975), a type of behaviour normally associated with the solitary bees and wasps. Presocial behaviour, in which one female looks after her own offspring, is a preliminary step in evolution of completely social behaviour (Wilson, 1975) and indeed the breeding behaviour of burying beetles bears a striking resemblance to the early stages of annual colony development by the bumble bee, Bombus sp. (Alford, 1971).

Care of the young by female Necrophorus may create more stable conditions for the development of the larvae. Physical aspects of the environment within the corpse may be stabilised by the crypt. This structure, although frequently observed (Fabre, 1919; Pukowski, 1933; Roussel, 1964a; Springett, 1967; Milne and Milne, 1976) has not yet been satisfactorily explained. There is some evidence from this study that the crypt may help to stabilise temperatures in the corpse, and investigation may show that other environmental factors, such as humidity, are similarly controlled. In the absence of such adaptations, physical conditions in the corpse may change dramatically. For example, the temperature of carrion may increase by 17°C due to the metabolic heat of the arthropods within it (Deonier, 1940; Payne, 1965; Wasti, 1972) and corpses can dry out in a few days (Wasti, 1972). The temperature in corpses buried by Necrophorus varies only by about 2½°C and as far as is known corpses remain moist for as long as larvae are present. It is believed that this is due to the crypt. Similar crypts have been described round the balls of dung buried by some dung beetles (Halffter, 1977). These may have a similar function to those of burying beetles, as it is known that burial of dung balls by tropical dung beetles prevents

temperature fluctuations in the ball, and prevents the dung drying out (Kingston and Coe, 1976).

Environmental stability together with parental care and provision for the larvae may reduce mortality of the young. Developmental mortality is lowest for the stages in the crypt and increases only when the larvae disperse from the corpse. In the soil, larvae are vulnerable to predators and environmental fluctuations. Pupae, for example, are preyed upon by Philonthus spp. (this study) and adults are taken by hedgehogs, Erinaceus europaeus L. (R.C. Welch, pers. comm.), owls (Elton, 1966; J. Mitchell, pers. comm.) and possibly by badgers. Predation of blowfly larvae also occurs after dispersal from the corpse (Putman, 1977).

Burying beetles differ from most other members of the carrion community in their ability to modify and stabilise a corpse. Some of the implications of this ability and the adaptations which lead to it may be studied by examination of the reproductive strategy of burying beetles.

The concept of reproductive strategy was introduced by MacArthur and Wilson (1967), who proposed that the response of organisms to different selection pressures leads to different reproductive strategies. Animals colonising unstable environments become r-selected, while those evolving in stable environments become K-selected. In r-selected organisms, reproductive effort is directed towards production of large numbers of small offspring with fast development and little parental care, whereas K-selected organisms produce fewer, larger young, with more investment in parental care, and a longer generation time (Pianka, 1970).

Carrion is an unpredictable, temporary habitat, and so should lead to the development of r-productive strategies (Southwood, 1975, 1977).

As an illustration of the adaptations expected in typical inhabitants of carrion, consider the Diptera, particularly the Calliphoridae, Sarcophagidae and Muscidae, which have evolved r-reproductive strategies to deal with temporary habitats (Beaver, 1977) (Table 6:2). Flies are highly mobile and are able to locate food very rapidly (Wigglesworth, 1965). Blowflies, for example, may be found laying eggs on a carcass immediately after the death of the animal (Wasti, 1972). These adaptations are necessary because of the unpredictable nature of carrion. Due to successional change, corpses may quickly become unsuitable for breeding and so the inhabitants of carrion must be able to exploit their habitat while it lasts, i.e. have a high fecundity, short generation time and low parental investment in the offspring. These characters are often associated with small size. Flies are small, rarely more than 1cm in size and have a high fecundity. For example, Musca vetustissima lays batches of 30 eggs at a time (Hughes and Walker, 1970), mature Phormia regina may contain more than 100 eggs (Stoffolano, 1974) and 100 - 300 eggs of Calliphora erythrocephela may be found on a single mouse (Putman, 1977). The female abandons the eggs immediately after laying, and may go on to lay eggs on another corpse (Hughes and Walker, 1970). Larval mortality is high, being 83% in Calliphora erythrocephala (Putman, 1973). Fly larvae develop rapidly, first instar blowfly larvae being found on carrion within 2 days of oviposition, with pupation starting to occur within six days (Wasti, 1972). The development of Calliphora erythrocephala from egg to pupa takes 8 days (Putman, 1977). In some species, e.g. Sarcophaga, development may be made even faster by larviposition (Beaver, 1977), growth of the larvae being complete within 4 - 7 days (Wasti, 1972). Blowflies may have several generations per year (Chinery, 1973). The rapid changes in carrion caused by fly larvae help to reduce intra- and inter-specific competition. Egg laying by

Table 6:2

The adaptations of r-strategists (blowflies) to living in carrion.

Adaptations expected in inhabitants of carrion	Adaptations of blowflies (typical r-strategists)
As habitat unpredictable, must be able to find habitat and disperse.	Highly mobile, able to find food quickly. Arrive rapidly, in large numbers at a corpse.
As habitat changes rapidly, must be able to breed quickly, often at low density. Must have high fecundity and low investment in parental care.	High fecundity, eggs abandoned by female.
	Development time short, reduced even further by larviposition in some species.
Usually associated with small size, low investment in interspecific competition mechanisms.	Several generations per year.
	Small in size.
	Competition a by-product of larval activities. No special mechanisms,

Consequences of r strategy on population

Unstable populations	- observed in fly populations
Catastrophic mortality	- observed in fly populations
Much density independent mortality	- observed in fly populations
Density dependent mortality in early stages of development (of scramble type)	- observed in fly populations

blowflies, for example, only occurs in the first few days after the death of an animal (Wasti, 1972; Putman, 1977, this study), and in Sarcophaga breeding in dead snails, larviposition is restricted to a period of less than a week (Beaver, 1971, 1977). Flies, therefore, have a low investment in special mechanisms for interspecific competition.

The development of an r-reproductive strategy usually has a number of effects on the animals population (Table 6:2). Catastrophic mortalities occur, largely density independent, and populations fluctuate greatly in size. Density dependent mortality usually occurs during the early stages of development (Stubbs, 1977), and is usually of the scramble type. These characteristics are observed in fly populations. For example, in Lucilia, fluctuations in the size of populations were observed in the laboratory, catastrophic density independent mortality occurred among adults and density dependent mortality of the scramble type took place among larvae when food was limiting (Nicholson, 1954). Similar density dependent mortality has been observed among the larvae of Calliphora erythrocephala (Putman, 1977), Musca vetustissima (Hughes and Walker, 1970), M.domestica, M.autumnalis and Orthellia caesurion (Wasti, Hosmer and Barney, 1975). Drosophila, a dipteran which breeds in another temporary habitat, rotting fruit, also suffers density dependent mortality among larvae (Bakker, 1961, 1969; Miller, 1964; Murai, 1975). In Sarcophaga spp., there is a density dependent decrease in pupal size as a result of competition (Beaver, 1977).

Despite some differences between species, all blowflies breeding on carrion are r-strategists (Denno and Lothran, 1976; Beaver, 1977). It would be expected that with the same selection pressure, burying beetles would have had to evolve similar strategies and would also be typical r-strategists. Examination of the characters of burying beetles

show that this is not completely so. In some respects Necrophorus is a typical r-strategist. The beetles are mobile, being powerful fliers (Schneider, 1975), can disperse widely, are known to fly long distances (Petrůska, 1964; Springett, 1967; this study), and can readily detect carrion by olfaction (Abbot, 1927; Shubeck, 1968). Beetles arrive very quickly at a corpse (Fabre, 1919; Milne and Milne, 1976; this study). Pheromone release by male Necrophorus may assist breeding at low densities (Pukowski, 1933; Springett, 1967). These adaptations are necessary to enable burying beetles to locate and breed on an unpredictable resource. Necrophorus is also a typical r-strategist in that it develops rapidly - an adaptation necessary for breeding in a temporary habitat. The time taken from egg to pupation in burying beetles is about 14 days. In other respects, however, Necrophorus is not a typical r-strategist (Table 6:3). Burying beetles are large, N.vespilloides the smallest being 1.6cm long, while N.germanicus at 4cm is one of the larger beetles of Europe. The fecundity of burying beetles is relatively low. There is only one generation each year, and, on average, 13 eggs are laid by N.vespilloides and 10 by N.investigator. There is a large parental investment in the offspring. Females provide an adequate source of food for the larvae, a stable environment, and remain with their offspring during their development to feed and protect them. As a result juvenile mortality is low. Necrophorus has evolved interspecific competition mechanisms, for example, the burial of the corpse and the various defence mechanisms, including warning colouration, release of fluid from crop and anus, and mimicry (Lane and Rothschild, 1965). In these adaptations, Necrophorus resembles a K-strategist. As far as is known, from this study and that of Springett (1967), burying beetle populations may also resemble those of a K-strategist. Breeding populations appear to remain relatively similar from year to year without major fluctuations.

Table 6:3

Adaptations of *Necrophorus* to breeding in carrion

Characteristics of r-strategist	Characteristics of K-strategist
Highly mobile	One pair take over corpse
Able to find food quickly	Relatively low fecundity
Arrive rapidly at a corpse	- few eggs
Development time within corpse	- one generation per year.
short.	High parental investment in offspring,
	larval mortality relatively low.
	Large size
	High investment in interspecific
	competition mechanisms.

Consequences of adaptations on population

Populations relatively stable?

Density dependent mortality among adults?

No density dependent mortality in larvae

Intraspecific competition for corpses of contest type.

Density dependent mortality may occur among adults, possibly prior to overwintering in N.vespilloides, and in both N.vespilloides and N.investigator prior to breeding. Density dependent mortality does not occur among larvae, possibly because females vary the number of eggs they lay to match the carrying capacity of the corpse. As far as breeding is concerned, intraspecific competition between adults for corpses is of the contest type.

Burying beetles use a combination of r- and K-strategies to exploit carrion. The adaptations characteristic of r-strategists are largely associated with the unpredictable nature of carrion, which the beetles cannot change, while those of the K-strategist reflect the modifications imposed on the temporary nature of the corpse by the actions of the beetles. By making a large investment in a few offspring, adult burying beetles ensure that most of their offspring survive. The number of young to be produced is set by the carrying capacity of the habitat. In this respect, the reproductive strategy of Necrophorus resembles that of many birds (Lack, 1966; Perrins and Moss, 1975). Although using different strategies, the productivity of blowflies and burying beetles, in terms of weight of adults produced, is similar (Table 6:4). The basic difference between the two types of strategy is that Necrophorus produces a few large adults, while Calliphora produces many, smaller adults.

Burying beetles are not the only insects to have evolved a K-strategy, although living in a temporary habitat. Similar adaptations have been evolved independently by dung beetles. It is of interest to compare the adaptations evolved by dung and burying beetles.

The evolution of dung burial can be traced more completely than can that of carrion. The trend is towards increasing care of the larvae and specialisation of behaviour (Halffter, 1977) (Table 6:5). The eggs

Table 6:4

Production of second generation adult Necrophorus vespilloides, N.investigator and Calliphoraerythrocephala on mouse corpses in the field.

Species	Mean no.eggs laid	Mean number adults produced	Mean total weight adults produced (mg)
N.vespilloides	12.87	9.44	1737.84
N.investigator	6.43	4.2	1311.58
C.erythrocephala +	(100-300)	55.02	1463.5

+ Data recalculated from Putman (1977 and pers. comm.)

Table 6:5

Behavioural adaptation of dung beetles

Dung buried under pat

Aphodius sp.	:	eggs laid in dung (Sandhall, 1975)
Geotrupes sp.	:	dung dragged into burrows under pat, eggs laid on dung (Chinery, 1973; this study).
Onthophagus sp.	:	dung dragged into burrows; dung made into balls; each ball food for one larva (Chinery, 1973)
Copris sp.	:	dung dragged under pat; young cared for until leave burrow. (Chinery, 1973)
Family Passalidae	:	parental care of young (Reyes-Castillo and Ritcher, 1973)

Dung removed from pat

Phaneus sp.	:	balls of dung rolled away from the pat; balls buried as food for one larva; one egg laid per dung ball; no parental care after provisioning egg. (Halffter, Halffter and Lopez, 1977).

of the least specialised dung beetles are laid directly in the dung, while more specialised species may care for the larvae until they complete their development. Some species roll balls of dung away from the mass, and bury them as discrete food units, each containing one egg. Those species which care for the young usually dig a crypt round the brood ball (Halffter, 1977). As in burying beetles, burial of dung leads to stabilisation of the environment for the larvae (Kingston and Coe, 1976), and prevents competition. Care of the young is associated with low developmental mortality (Halffter, 1977) and reduced fecundity. In these respects, the K-strategies of dung and burying beetles are almost identical, and are a striking example of parallel evolution. When the methods of reducing fecundity used by dung and burying beetles are compared, differences are observed. In dung beetles, increasing parental care of the offspring is associated with a decrease in the number of ovarioles, and in the number of eggs laid (Table 6:6). The least specialised dung beetles, e.g. the Geotrupidae, have 12 ovarioles (six in each ovary). The most advanced dung beetles of the sub-family Scarabaeinae, have only a single ovariole and lay only one egg at a time. This is associated with a high degree of complexity in the nesting behaviour and care of the larvae, one egg being placed in each dung ball. Further, within this sub family there is a reduction in the number of eggs produced by the single ovariole, depending on the complexity of nesting behaviour (Halffter and Lopez, 1977)(Table 6:6). Such adaptations are not observed in burying beetles, which have the same number of ovarioles as do the least specialised of the Silphidae (Table 6:7). The difference in adaptation between carrion and dung beetles may be due to the different natures of the substrates on which they live. Unlike carrion, pieces of dung can be broken off, and it is possible for the dung beetle to provision each egg separately. Therefore only one egg need be laid at a time, and so only one ovariole is needed. Carrion must

Table 6:6.

Variation in fecundity of dung beetles

Group	Behaviour	No. of ovarioles[+]
Geotrupidae	No parental care	6 - 6
Passalidae	Parental care	2 - 2
Scarabaeidae		
- Aphodiinae	no parental care	2 - 2 to 7 - 7
- Scarabaeinae	nest building, provision of food for young	1 - 0

Number of eggs laid by Scarabaeinae:

Onthophagus gazella	least complex nesting behaviour	130 eggs
Phaneus mexicana	complex nesting behaviour	12 eggs
P.daphnis	complex nesting behaviour	7.3 eggs

[+](Basic number of eggs in the Scarabaeidae is 6 - 6

i.e. six ovarioles in each ovary. Ritcher and Baker, 1974).

Table 6:7

Number of ovarioles in Silphidae

Species	Number of ovarioles
Phosphuga atrata +	7 - 7
Oeceoptoma thoracica +	7 - 7
Silpha spp. +	7 - 7 to 12 - 12
Thanatophilus sinuatus +	12 - 12
Necrophorus vespilloides	8 - 8
Necrophorus investigator	12 - 12

+ (From Suzzoni, 1973).

be buried in one piece, and so all the larvae must be reared together and all the eggs laid at the same time.

Although there are some differences in detail, both dung and burying beetles have evolved similar K-reproductive strategies to exploit the same type of unpredictable, temporary habitat. As they make use of different resources, there is little potential for competition between dung and burying beetles. Both types of beetle must compete for their particular resource with the r-selected blowflies. The evolution of a symbiotic relationship between burying beetles and the mite Poecilochirus necrophori specifically to remove dipterous eggs and larvae from carrion (Springett, 1967, 1968), has already been discussed. Dung beetles too compete with flies (Ferrat, 1973, MacQueen, 1975, MacQueen and Beirne, 1975), and it is possibly no coincidence that the mite Parasitus coleoptratorum is found to have a relationship with dung beetles such as Geotrupes (Rapp, 1959).

Although burying beetles resemble other insects in some aspects of their ecology, such as interspecific competition, in other respects they differ. As far as reproductive strategies are concerned, burying beetles do not fit into any rigid framework. While comparisons may be drawn with other species, it is not always possible to draw up rules governing the responses of animals to a particular set of circumstances. Each species and its responses to the environment must be considered independently, without preconceived ideas about what it should or should not do.

Despite the complexities of its behaviour and ecology, Necrophorus is basically a decomposer. As such it is limited by the resources it requires, and which are provided by the habitat (Hairston, Smith and Slobodkin, 1960). Within these limitations, Necrophorus is

an animal which makes the best use of the resources available to it. A study of the ecology of burying beetles can provide an insight not only into the decomposer community and its function, but also into many other aspects of ecology. Further, as all elements in the food web are ultimately linked through the carrion community, the activities of the burying beetle, and animals like it, allow the existence of other, perhaps more attractive and easily studied animals. Although often neglected, the study of decomposer organisms is perhaps one of the most fundamental in ecology. Necrophorus may be regarded as one of the most highly specialised and effective members of this community and the importance of further studies on this fascinating and beautiful animal should not be underestimated.

REFERENCES

Abbott, C.E. (1927a). Experimental data on the olfactory sense of Coleoptera, with special reference to the Necrophori. Ann. ent. soc. Amer. 20 207-216.

Abbot C.E. (1927b). Further observations on the olfactory powers of the Necrophori. Ann. ent. soc. Amer. 20 550-553.

Abbot, C.E. (1937). [The necrophilus habit in Coleoptera.] Bull. Brooklyn ent. Soc. 32 202-204.

Akopyan, M.M. (1953). The fate of corpses of ground squirrels (susliks) on the steppe . Zool. Zh. 32 1014-1019.

Alford, D.V. (1971). Egg laying by bumble bee queens at the beginning of colony development. Bee World 52 11-18.

Arnett, R.H. (1944). A revision of the Nearctic Silphini and Nicrophorini based upon the female genitalia. (Coleoptera, Silphidae). J. New York ent. soc. 52 1-26.

Arnett, R.H. (1946a). A new species of Nicrophorus from the Phillipine Islands (Coleoptera Silphidae). Proc. ent.soc. Wash. 48 207-209.

Arnett, R.H. (1964b). Coleoptera notes. I : Silphidae. Can. Ent. 78 131-134.

Arnett, R.H. (1947). Coleoptera notes. II : Silphidae. Can. Ent. 79 110-112.

Arnett, R.H. (1950). The Silphidae of the Phillipine Islands (Coleoptera). Proc. ent. soc. Wash. 52 63-69.

Bakker, K. (1961). An analysis of factors which determine success in competition for food among larvae of Drosophila melanogaster. Arch. néerl. Zool. 14 200-231.

Bakker, K. (1969). Selection for rate of growth and its influence on competition ability of larvae of Drosophila melanogaster. Neth. J. Zool. 19 541-595.

Batten, L.A. (1973). Population studies of suburban blackbirds. Bird Study 20 251-258.

Beaver, R.A. (1971). Ecological studies on Diptera breeding in dead snails. I : Biology of the species found in Cephaea nemoralis (L.). Entomologist 105 41-52.

Beaver, R.A. (1973). The effects of larval competition on puparial size in Sarcophaga spp. (Dipt : Sarcophagidae) breeding in dead snails. J. Ent. (A) 48 1-9.

Beaver, R.A. (1974). Intraspecific competition among bark beetle larvae. (Copeoptera : Silphidae). J. Anim. Ecol. 43 455-467.

Beaver, R.A. (1977). Non equilibrium 'Island' communities : Diptera breeding in dead snails. J. Anim. Ecol. 46 783-798.

Bennettová - Řežábová, B. (1972). The regulation of vitellogenesis by the central nervous system in the blow fly Phormia regina (Meigen). Acta Entomol. Bohemoslov. 69 78-83.

Birch, L.C. (1948). The intrinsic rate of natural increase of an insect population. J. Anim. Ecol., 17 15-26.

Birch, L.C., Park, T. and Frank, P.W. (1951). The effect of intraspecific and interspecific competition on the fecundity of two species of flour beetle. Evolution 5 116-132.

Birch, M.C. (1967). Range and habitat of Necrodes littoralis L. (Col. Silphidae). Ent. mon. Mag. 103 216.

Birkett, N.L. (1969a). Inland records of Necrodes littoralis, Col. Silphidae. Ent. mon. Mag. 104 90.

Birkett, N.L. (1969b). Inland records of Necrodes littoralis Col. Silphidae. Ent. mon. Mag. 105 213.

Birkett, N.L. (1973). Inland records of Necrodes littoralis Col. Silphidae. Ent. mon. Mag. 109 190.

Bliss, R.Q. (1949). Studies on the Silphidae. I. Secondary sexual differences in the genus Nicrophorus (Coleoptera). Ent. News. 60 197-204.

Boeckh, J. (1962a). Elektrophysiologische untersuchungen an einzeln Geruchtsrezeptoren auf den Antenem des Totengrabers (Necrophorus: Coleoptera). Zeitschr. für vergl. Physiol. 46 212-248.

Boeckh, J. (1962b). Elektrophysiologische untersuchungen einzelner Reichsensillen von Kafern. Zool. Anz. 26 297-301.

Brewer, J.W. and Bacon T.R. (1975). Biology of the carrion beetle Silpha ramosa Say. Ann. ent. soc. Amer. 68 786-790.

Brian, M.V. (1952). The structure of a dense natural ant population. J. Anim. Ecol. 21 12-24.

Brivio, C. (1953). Studi sui Necrophorini (Coleoptera : Silphidae) : I. Il Necrophorus germanicus in Lombardia. Natura 44 85-88.

Calow, P. (1977). Conversion efficiencies in heterotrophic organisms. Biol. Rev. 52 385-409.

Cantonnet, F. and Lecordier, C. (1947). Note biologique sur les Nécrophores en forêt d' Andaine (L'Crne). L' Entomol. 3 134-136.

Caughley, G. and Birch, L.C. (1971). Rate of increase. J. Wildl. Man. 35 658-663.

Chaplin, R.G. (1977). 'Deer' Blandford. Poole.

Chapman, R.F. and Sankey, J.H. (1955). The larger invertebrate fauna of three rabbit corpses. J. Anim. Ecol. 24 395-402.

Chinery, M. (1973). 'A field guide to the insects of Britain and Northern Europe'. Collins, London.

Clark, C.U. (1895). On the food habits of certain dung and carrion beetles. J. New York ent. soc. 3 61.

Clark, P.J. and Evans, F.C. (1954). Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35 445-453.

Connel, J.H. (1961a). The influence of interspecific competition and other factors on the distribution of the barnacle Chthalamus stellatus. Ecology 42 710-723.

Connell, J.H. (1961b). Effects of competition predation by Thais lapillus and other factors on natural populations of the barnacle Balanus balanoides. Ecol. Mon. 31 61-104.

Corbet, G.B. and Southern, H.N. (1977). 'The handbook of British mammals' 2nd Edition Blackwell : Oxford.

Cousins, S. (1976). A preliminary checklist of British breeding bird weights. Unpublished report : British Trust for Ornithology.

Cramp, S. (1955). Breeding of the willow warbler. Bird Study 2 121-135.

Crombie, A.C. (1944). On intraspecific and interspecific competition in larvae of graminivorous insects. J. exp. Biol. 20 135-151.

Crombie, A.C. (1945). On competition between different species of graminivorous insects. Proc. roy Soc. (B) 132 362-395.

Crombie, A.C. (1947). Interspecific competition. J. anim. Ecol. 16 44-73.

Crowcroft, A.C. (1957). 'The life of the shrew' Max Rheinhardt : London.

Crowson, R.A. (1955). 'The natural classification of the families of Coleoptera'. Nathaniel Lloyd, London.

Curtis, D.J. (1976). Loch Lomond National Nature Reserve : status of araneid and phalangid communities. Report published by Nature Conservancy Council, S.W. Scotland Region.

Delahon, P. (1925). Nachtrage zy 'Schliskys Systematischen Verzeichnis der Kafer Deutschlands' von 1909 mit besonder Berüchsichtigung der Formen der Mark Brandenburg, sowie einig sOnstige Bemerkungen ueber Kafer aus Deutschland. D. ent. Zs. Berlin 5 305-308.

Denlinger, D.L. and Ma, W.C. (1974). The pregnancy cycle in G.morsitans. J. Ins. Physiol. 20 1015-1026.

Denno, R.F. and Cothran, W.R. (1976). Competitive interactions and ecological strategies of sarcophagid and calliphorid flies inhabiting rabbit carrion. Ann. ent. soc. Amer. 69 109-113.

Deonier, C.C. (1940). Carrion temperatures and their relation to winter blowfly populations and activity in the southwest. J. Econ. Entomol. 30 166-170.

Dethier, V.G. (1947). The role of antennae in the orientation of carrion beetles to odours. J. New York ent. soc. 55 285-293.

Dethier, V.G. (1961). Behavioural aspects of protein ingestion by the blowfly Phormia regina Meigen. Biol. Bull. mar. biol. lab. Woods Hole. 121 456-470.

Dibb, J.R. (1948). 'Field book of Beetles'. Brown and Son, London.

Dixon, A.F.G. (1973). 'The Biology of Aphids' Edward Arnold, London.

Duffey, E. (1968). Ecological studies on the large copper butterfly, Lycaena dispar Haw. batavus Obth. at Woodwalton Fen National Nature Reserve. J. Appl. Ecol. 5 69-96.

Duffey, E. (1977). The re-establishment of the large copper butterfly Lycaena dispar batavus Obth. on Woodwalton Fen National Nature Reserve, Cambridgeshire, England, 1969-1973. Biol. Cons. 12 143-158.

Dumortier, B. (1963). Sound emmission apparatus in Coleoptera. In : Busnel R.G. (ed.) 'Acoustic behaviour of animals'. Elsevier, Amsterdam.

East, K. (1964). Small mammal trapping on Inchcailloch and Torrinch. Unpublished internal report, Nature Conservancy, Balloch.

Edgar, W.D. and Meadows, P.S. (1969). Case construction,movement, spatial distribution and substrate selection in the larvae of Chironomus riparius Meigen. J. exp. Biol. 50 247-253.

Elliot, G.F.S., Laurie, M. and Murdoch, J.B. (1901). 'Fauna, flora and geology of the Clyde Area'. British Association for Advancement of Science, Glasgow.

Elton, C.S. (1966). 'The pattern of animal communities'. Methuen, London.

Emetz, V. and Schawaller, W. (1975). Silphidae aus dem Nepal-Himalaya. Senckenbergiana Biol. 56 221-231.

Ernst, K.D. (1969). Die Feinstruktur von Reichsensillan auf der Antenne des Aaskäfers, Necrophorus (Coleoptera). Z. Zellforsch. Mikrosk. Anat. 94 72-102.

Ernst, K.D. (1972a). Die Ontogeny der basiconischen Reichsensillen auf der Antenne von Necrophorus (Coleoptera). Z. Zellforsch. Mikrosk. Anat. 129 217-236.

Ernst, K.D. (1972b). Sensillum coelosphaericum, die Feinstruktur einer neuen olfactorischen Sensillentyps. Z. Zellforsch. Mikrosk. Anat. 132 95-106.

Fabre, J.H. (1919). 'The glow worm and other beetles'. London.

Ferrar, P. (1973). The CSIRO Dung beetle project. Wool Tech. and Sheep Breeding. 20 73-75.

Fichter, G.S. (1949). Necrophily vs. Necrophagy. Ohio Journ. of Science. 49 201-204.

Fisher, R.A. and Yates, F. (1963). 'Statistical tables for Biological, Agricultural and Medical Research'. 6th Edition. Oliver and Boyd, London.

Flegg, J.J.M. and Bennett, T.G. (1974). 'The birds of oak woodlands'. In: M.G. Morris and F.H. Perring (eds.) 'The British Oak: its history and Natural History' E.W. Classey, Faringdon.

Fox, J.L. (1976). Falling bird populations. The Flycatcher. 26 2.

Frank, P.W. (1952). A laboratory study of intraspecies and interspecies competition in Daphnia pulicariae (Forbes) and Simocephalus vetulus O.F. Muller. Physiol. Zool. 25 178-204.

Frank, P.W. (1957). Coactions in laboratory populations of two species of Daphnia. Ecology 38 510-519.

Fullager, P.J., Jewell, P.A., Lockley, R.M. and Rowlands, I.W. (1963). The Skomer vole Clethrionomys glareolus skomerensis and the long tailed field mouse Apodemus sylvaticus on Skomer Island Pembrokeshire in 1960. Proc. Zool. Soc. Lond. 140 295-314.

Fuller, M.W. (1934). The insect inhabitants of carrion - a study in animal ecology. Austr. Council Sci. Ind, Res. 82 5-62.

Gause, G.F. (1934). 'The struggle for existence' Wilkins and Wilkins, Baltimore.

Gersdorf, E. (1969). Käfer (Coleoptera) aus dem Iungtertiar Norddeutschlands. Geol. Jb. 87 295-331.

Gersdorf, E. (1970). Der Ei-Ablage-Apparat der Necrophorini. Faun. Okol. Mitt. 3 364-368.

Hairston, N.G., Smith, F.E. and Slobodkin, L.E. (1960). Community structure, population control and competition. Am. Nat. 94 421-425.

Halffter, G. (1977). Evolution of nidification in the Scarabaeinae (Coleoptera, Scarabaeidae). Quaest. Entomol. 13 231-253.

Halffter, G. and Lopez, Y.G. (1977). Development of the ovary and mating behaviour in Phanaeus. Ann. ent. soc. Amer. 70 203-213.

Halffter, G. Halffter, V. and Lopez, I.G. (1974). Phanaeus behaviour : food transportation and bisexual cooperation. Environ. Entomol. 3 341-345.

Hartley, P.H.T. (1967). Parental care in the song thrush. Birds 1 271-273.

Hassell, M.P. (1975). Density dependence in single species populations. J. Anim. Ecol. 44 283-295.

Hassell, M.P. and Huffaker, C.B. (1969). Regulatory processes and population cyclicity in laboratory populations of Anagasta kühniella (Zeller) (Lepidoptera : Phycitidae) : III. The development of population models. Res. popul. ecol. 11 186-210.

Hassell, M.P., Lawton, J.H. and May, R.M. (1976). Patterns of dynamical behaviour in single species populations. J. Anim. Ecol. 45 471-486.

Hatch, M.H. (1925). Habitats of Coleoptera. J. New York ent. soc. 33 217-223.

Hatch, M.H. (1927a). Studies in the carrion beetles of Minnesota, including new species. Tech. Bull. Univ. Minnesota Agric. Expt. Sta. St. Paul 48 1-19.

Hatch, M.H. (1927b). Studies on the Silphinae. J. New York ent, soc. 35 331-370.

Hatch, M.H. (1928). Silphidae II. Coleop. Catalog 95 63-244.

Hatch, M.H. (1932). 'Necrophorus' or 'Nicrophorus'. J. New York ent. soc. 40 391.

Hatch, M.H. (1940). Observations in Silphinae with a note on intraspecific variations and designations. J. New York ent. soc. 48 233-244.

Hatch, M.H. (1946). Mr. Ross H. Arnett's 'Revision of the Neartic Silphini and Nicrophorini.' J. New York ent. soc. 54 99-103.

Herman, L.H. (1964). Nomenclatural considerations of Nicrophorus (Coleoptera : Silphidae). Coleopt. Bull. 18 5-6.

Hinton, H.E. (1969). Diffraction gratings in burying beetles (Nicrophorus). Entomologist 102 185-189.

Hlavac, T.E. (1975). The prothorax of Coleoptera (except Bostrichiformia-Cucujiformia). Bull. Mus. Comp. Zool. 147 137-183.

Hlisnikowski, J. (1929). Ueber die bis jezt bekannten Färbungsabarten des Necrophorus vestigator Hersch und antennatus Beitt. Ent. Nachr. Bl. 3 119-120.

Hlisnikowski, J. (1932). Zwei neue Arten der Gattung Necrophorus Fab. (Col. Necrophorini) nebst einer Bestimungstabelle der mir bekannten Arten der paläarktischen Fauna. Coleopt. Centralbl. 6 22-30.

Hlisnikowski, J. (1942). Coleopterogische Notizen. Mitt München ent. Ges. 32 578-579.

Hlisnikowski, J. (1964a). 3u 4 Beitrag zur Kenntnis der Gattung Necrophorus F. (Coleoptera : Silphidae). Reichenbachia 3 223-5, 241-5.

Hlisnikowski, J. (1964b). Eine neue Necrophorus Art aus Thailand (Coleoptera : Necrophorini). 5. Beitrag zur Kenntnis der Gattung Necrophorus F. Reichenbachia 4 131-132.

Hofmann, E. (1902). "The young beetle collectors handbook". Swan Sonnenschein, London.

Horn, G.H. (1880). Synopsis of the Silphidae of the United States with reference to the genera of other countries. Trans. ent. soc. Amer. 8 219-322.

Hornung, H. and Mew, G. (1970). Report of the soils of the island of Inchcailloch, Loch Lomond National Nature Reserve. Unpublished internal report. Nature Conservancy, Balloch

Horrill, A.D., Sykes, J.M. and Idle, E.T. (1975). The woodland vegetation of Inchcailloch, Loch Lomond. Trans. bot. Soc. Edinb. 42 307-334.

Hughes, R.D. (1974). Variation in the proportion of different reproductive stages of female bush flies (Musca vetustissima Wlk. Diptera, Muscidae), in bait catches as a cause of error in population estimates. Bull. ent. Res. 64 65-71.

Hughes, R.D. and Walker, J. (1970). The role of food in the population dynamics of the Australian bushfly. In A. Watson (ed.) 'Animal populations in relation to their food resources'. Brit. Ecol. Soc. Symp. 10 pp 255-269. Blackwell, Oxford.

Humphreys, W.F. (1973). Ecological energetics of Geolycosa godaffroyi (Areneae : Lycosidae) with an appraisal of production efficiency in ectothermic animals. J. Anim. Ecol. 47 627-652.

Hussey, N.W. and Lane, J. (1967). Necrophagous Coleoptera trapped in different habitats in Midlothian. Ent. mon. mag. 92 201.206.

Hutchinson, G.E. (1957). Concluding Remarks. Cold Spr. Harb. Symp. Quant. Biol. 22 415-427.

Idle, E.T. and Mitchell, J. (1963). The fallow deer of Loch Lomondside. Deer 1 7.

Illingworth, J.F. (1927). Insects attracted to carrion in Southern California. Proc. Haw. entomol. Soc. 6 201-203.

Imms. A.D. (1959). 'Outlines of Entomology' 5th Edition Methuen, London.

Jacobson, G. (1924). Annotationes synonymicae et systematique de Coleoptera. Rev. russe . Ent. 18 237-244.

Jewell, P.A. (1965). New research in the vole and field mouse of Skomer. Nature in Wales 9 103-109.

Jewell, P.A. (1966). Breeding season and recruitment in some British mammals confined on small islands. Symp zool Soc. Lond. 15 89-116.

Johnson, W.F. and Halbert, J.N. (1902). A list of the beetles of Ireland. Roy. Irish Acad. Proc. Ser. III. 6 535-327.

Jolly, G.M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52 225-247.

Joy, N.H. (1932). 'Practical handbook of British beetles' Witherby, London.

Kamimura, K., Nakane, T. and Koyama, N. (1964). Seasonal and altitudinal distribution of beetles in Mt. Jônen - the Japan Alps, with descriptions of new species. I (Studies in the insects of high mountains III). Scien. Rep. Kyoto prefect. Univ. 4 17-38.

Kanabé, D. (1935). Zwei neue Käferabesrationem. Ent. Nachr. Bl. 9 64.

Kaufmann, R.R.V. (1931). Beetles associated with carrion in Pannel Ash, Nr. Harrogate. Ent. mon. Mag. 73 78-81, 227-232, 268-272.

Kaufmann, R.R.V. (1941). British carrion beetles. Naturalist 1941 63-72, 115-124, 133-138, 149-156.

Kay, D., Rothschild, M. and Aplin, R. (1969). Particles present in the haemolymph and defensive secretions of insects. J. Cell Sci. 4 369-379.

Kieseritzky, V. (1930). Silphidae (Coleoptera). Abh. Pamir Exped. (1928) 2 59-63.

Kingston, T.J. and Coe, M. (1976). The biology of a giant dung beetle (Heliocopris dilloni) (Coleoptera : Scarabaeidae). J. Zool. 181 243-252.

Kloet, G.S. and Hinks, W.D. (1945). 'Checklist of British Insects' Kloet and Hinks, Stockport.

Klomp, H. (1962). The influence of climate and weather on mean density level, the fluctuations and the regulation of animal populations. Arch. néerl. de Zool. 15 68-107.

Klomp, H. (1964). Intraspecific competition and the regulation of insect numbers. Ann. Rev. Ent. 9 17-40.

Kôno, H. (1929). Beitrag zur Silphiden Fauna Japan. (Col.). Insecta matsum. 3 157-165.

Kryzhanovskiy, J. (1971). Novye dlya fauny S.S.S.R. Zestkokrylyye (Coleoptera) iz Primor' ya i zoogeograficheskoye znacheniye etikh nakhodok. Zool. Zh. 50 210-214.

Lack, D. (1966). 'Population studies of birds'. Clarendon, Oxford.

Lane, C. and Rothschild, M. (1965). A case of Müllerian mimicry of sound. Proc. E. ent. Soc. Lond (A) 40 156-158.

Leech, H.B. (1935). The family history of Nicrophorus conservator Walker. Proc. ent. Soc. Br. Columb. 31 36-40.

Leech, H.B. (1937). Notes on certain names in use in the vespilloides group of Nicrophorus Fab. (Coleoptera L Silphidae). Bull. Brooklyn ent. Soc. 32 156-159.

Lengerken, H. von. (1938). Bezeihungen zwischen der Ernährungzweise und der Gestaltung der Mandibeln bei den larven der Silphini (Coleopt.) Zool. Anz. 122 171-175.

Lengerken, H. von. (1939). Die Brufürsoge und Brutflegeinstinkte der Käfer. Ergeben Insektenbiol. 1 (Leipzig Akad. Verlages).

Leslie, P.H., Chitty, D. and Chitty, H. (1953). The intimation of population parameters from data obtained by means of the capture-recapture method. III. An example of the practical application of the method. Biometrika. 40 137-169.

Likovský, Z. (1967). Beitrag zur Kenntnis der Aasenfauna (Insecta : Coleoptera). Pr. kraj. Mus. Hradci. 8 97-116.

Ling, R.T. (1957). Burying beetles. Countryside (N.S.) 18 58-64.

Lock, M.A. and Reynoldson, T.B. (1976). The role of interspecific competition in the distribution of two stream dwelling triclads, Crenobia alpina (Dana) and Polycelis felina (Dalyell), in North Wales. J. Anim. Ecol. 45 581-592.

Lotka, A.J. (1932). The growth of mixed populations : two species competing for a common food supply. J. Wash. Acad. Sci. 22 461-469.

MacArthur, R.H. (1958). Population ecology of some warblers of North Eastern coniferous forests. Ecology 39 599-619.

MacArthur, R.H. and Wilson, E.O. (1967). 'The theory of island biogeography'. Princeton University Press, Princeton.

MacDonald, J.G. (1974). Geology In R. Tippett (ed.) 'A Natural History of Loch Lomond'. University of Glasgow Press. Glasgow.

MacFadyen, A. (1963). 'Animal Ecology : Aims and Methods' Pitman, London.

McGhehey, J.H. (1971). Female size and egg production of the mountain pine beetle, Dendroctonus ponderosae Hopkins. Info. Rep. Nth. For. Res. Cent. Edmonton. NOR-X-9.

MacKerras, M.J. and Freney, M.R. (1933). Observations on the nutrition of maggots of Australian blowflies. J. exp. Biol. 10 237-246.

MacLeod, J. (1943). A survey of British sheep blowflies. Bull. ent. Res. 34 65-88.

MacQueen, A. (1975). Dung as an insect food source - dung beetles as competitors of other coprophagous fauna and as targets for predators. J. Appl. Ecol. 12 821-327.

MacQueen, A. and Beirne, B.P. (1975). Dung burial activity and fly control potential of Onthophagus nuchicornis (Coleoptera : Scarabaeinae) in British Columnia. Can. Ent. 107 1215-1220.

Marikovskiy, P. (1974) [Insects as enemies of Bradybaena : Mollusca] Ekologiya 5 69-70.

Mazokhin-Porshnyahov, G.G. (1953). Coleoptera, Necrophorini of N.E. China. Zool. Zhurn. 32 235-237.

Mellanby, K. (1973). 'Mammalia' In R.C. Steele and R.C. Welch (Eds.) 'Monks Wood : a nature reserve record.' The Nature Conservancy, Natural Environment Research Council, Huntingdon.

Meserve, F.G. (1936). The Silphidae of Nebraska. Ent. News. 47 132-134.

Mikšić, R. (1971). Beitrag zur Verbreitungskenntnis der Silphidae (Coleoptra - Staphylinoidea) in Jugoslavien. Ocat. Entomol. Jugoslav. 7 57-64.

Miller, R.S. (1964). Larval competition in Drosophila melanogaster and D.simulans. Ecology 45 132-148.

Miller, T.A. and Treece, R.E. (1968). Some relationships of face fly breeding, ovarian development and incidence in dairy cattle. J. econ. Ent. 61 250-257.

Millican, C.W. (1965). Insect succession in carrion. Unpublished B.Sc. Thesis, University of Glasgow.

Milne, L.J. and Milne, M.J. (1944). Notes on the behavior of burying beetles (Nicrophorus spp.). J. New York ent. Soc. 52 311-327.

Milne, L.J. and Milne, M.J. (1976). The social behavicur of burying beetles. Sci. Am. 236 84-89.

Mitchell, J. (1974). Mammals. In R. Tippett (Ed.) 'A Natural History of Loch Lomond' University of Glasgow Press, Glasgow.

Moore, B.P. (1955). Notes on Carrion Coleoptera in the Oxford district. Ent. mon. Mag. 91 292-295.

Mosebach-Pukowski, E. (1936). Gibt es einen sozialen Instinkt bei Necrophorus. Forsch. u. Fortschr. 12 38-39.

Mroczkowski, M. (1949). Notes of successive appearance of some species of the genus Nicrophorus Fabr. and Neonicrophorus Hatch. (Col. Silphidae). Polsk. Pismo ent. 19 196-199.

Mroczkowski, M. (1959). Nicrophorus (Nicrophorus)kieticus sp. n. from the Solomon Islands (Coleoptera : Silphidae). Ann. Zool. 18 65-69.

Murai, M. (1975). Theoretical studies on the role of food exploitation for the competition of the scramble type. Res. Popul. Ecol. (Kyo). 16 289-308.

Murray A. (1853). 'A catalogue of the Coleoptera of Scotland' Blackwood, Edinburgh.

Newton, A. and Peck, S.B. (1975). Baited pitfall traps for beetles (Col.) Coll. Bull. 2º 45-46.

Newton, I. (1972). 'Finches' Collins, London.

Newton, I. and Moss, D. (1977). Breeding birds of Scottish pine woods. In R.G.H. Bunce and J.N.R. Jeffers (Eds.) 'Native Pinewoods of Scotland' pp. 26-31. Natural Environment Research Council - Institute of Terrestrial Ecology, Cambridge.

Nicholson, A.J. (1954). An outline of dynamics of animal populations. Aust. J. Zool. 2 8-65.

Nickle, W.R. (1970). A taxonomic review of the genera of the Apelenchoidea (Fuchs 1937) Thorne 1949 (Nematode : Tylenchida). J. Nematol. 2 375-392.

Nickle, W.R. (1972). Nematode parasites of insects. Proc. Ann. Tall Timbers Conf. 1972 145-163.

Nickle, W.R. (1973). Identification of insect parasitic nematodes : a review. Exp. Parasit. 33 303-317.

Niemitz, C. (1972). Bioakustische, verhaltenphysiologische und morphologische Untersuchungen an Necrophorus vespillo (Fabr). Forma et Functio 5 209-230.

Niemitz, C. and Krampe, A. (1971). Gëhorsinn bei polyphagen Käfern nachgewiesen. Die Naturwissenschaften 58 368-369.

Niemitz, C. and Krampe, A. (1972). Untersuchungen zum Orientierungsverhalten der Larven von Necrophorus vespillo F. (Silphidae : Coleoptera). Z. Tierpsychol. 30 456-463.

Novák, B. (1964a). Fallenfang und Synokologie (Col. Silphidae et Carabidae). Proc. 12th int. Congr. Ent. 1964 423-429.

Novák, B. (1964b). Isolation als Ausschaltungsfaktor in den Phänomenon der Kaskurrenz bei den Totengräbern (Col. Silphidae). Sb. Pracĭ přir Fak. palack Univ. Olomouci (Biol VI) 16 147-158.

Novák, B. (1965a). Zur Faunistik und Okologie der Totengraber in den Feldbiotopen von Hana (Col. Silphidae). Sb. Pracĭ přir Fak. palack Univ, Olomouci (Biol. VII) 19 121-152.

Novák, B. (1965b) Abundanzänderungen unserer Feldbewohnenden Totengräber als Folge der Dezimierung durch den Fallenfang. (Col. Silphidae) Sb. Pracĭ přir Fak. Palack, Univ. Olomouci (Biol VII). 19 99-119.

Orr, C.W.M. (1964a). The influence of nutritional and hormonal factors on egg development in the blowfly Phormia regina (Meig.). J. Ins. Physiol. 10 53-64.

Orr, C.W.M. (1964b). The influence of nutritional and hormonal factors on the chemistry of the fat body, blood and ovaries of the blowfly, Phormia regina (Meig.). J. Ins. Physiol. 10 103-119.

Pardo-Alcaide, A. and Yus, R. (1974). Genera de Coleópteros de la Peninsula Ibérica. Familia Silphidae. Graellsia 30 93-111.

Park, T. (1943). Experimental studies of interspecies competition : I. Competition between populations of the flour beetles Tribolium confusum Duval and Tribolium castaneum Herbst. Ecol. Mon. 18 265-308.

Park, T. (1954). Experimental studies of interspecies competition : II. Temperature, humidity and competition in two species of Tribolium. Physiol. Zool. 27 177-238.

Paulian, R. (1946). Essai de bionomie quantitative sur les Nécrophores (Col. Silphidae). Rev. franç Ent. 13 93-8.

Payne, J.A. (1965). A summer carrion study of the baby pig, Sus scrofa Linnaeus. Ecology 46 592-602.

Payne, J.A. (1967). A comparative ecological study of pig carrion decomposition and animal succession with special reference to the insects. Diss. Abst. 28 (B) 1734.

Pernetta, J.C. (1976). Diet of shrews Sorex araneus L. and Sorex minutus L. in Wytham grassland. J. Anim. Exol. 45 899-912.

Perrins, C.M. and Moss, D. (1975). Reproductive rates in the great tit. J. Anim. Ecol. 44 695-706.

Pessôa, S.P. and Lane, F. (1941). Coleopteros necrofagos de interésse médíc-legal. Arq. Zool. 2 389-504.

Petrůska, F. (1964). Beitrag zur Bewegungsaktivität einiger Aaskäferarten (Col. Silphidae et Histeridae). Sb. Prací přir Fak. palack. Univ. Olomouci (Biol. VI). 16 159-189.

Peyerimkoff, P. de (1934). Les Necrophorus (Col. Silphidae) en Berberie. Bull. Soc. Hist. Nat. Afr. N. 25 333-334.

Pianka, E.R. (1970). On r- and K-selection. Am. Nat. 104 592-597.

Pic, M. (1933). Coléoptères exotiques en partie nouveaux. Echange (Moulins). 49 1-15.

Placido, C. (1971). Survey of small mammals on Inchcailloch. Unpublished internal report. Nature Conservancy, Balloch.

Plant, C.W. (1976). Some observations on the winter diet of the Barn Owl (Tyto alba) on Skomer Island, Dyfed Wales. Nature in Wales 15 54-59.

Podoler, H. and Rodgers, D. (1975). A new method for the identification of key factors from life table data. J. Anim. Ecol. 44 85-114.

Pontin, J. (1961). Population stabilisation and a comparison between the ants Lasius flavus and L.niger. J. Anim. Ecol. 30 47-54.

Pontin, J. (1963). Further considerations of competition and the ecology of the ants Lasius flavus and L.niger. J. Anim. Ecol. 32 565-574.

Pontin, J. (1969). Experimental transplantation of nest mounds of Lasius flavus in a habitat containing L.niger and Myrmica scabrinoides. J. Anim. Ecol. 38 747-754.

Portevin, G. (1926a). Les Grandes Nécrophages du Globe : Silphini - Necrodini - Necrophorini. In P. Lechavalier Ed. 'Encyclopedie Entomologique VI' pp. 1-270. Paris.

Portevin, G. (1926b). Description de deux Silphides nouveaux de Nouvelle Guinée. Nova Guinea. 15 (Zool.) 210-211.

Portevin, G. (1943). Silphida nouveaux ou petits connus (Coleoptera). Rev. franç Ent. 10 47-48.

Prokopic, J. and Svatopluk, B. (1975). Beetles (Coleoptera) as new intermediate hosts of helminths. Vestn. Cesk. Spol. Zool. 39 224-230.

Pukowski, E. (1933). Ökologische Untersuchungen an Necrophorus F. Zeit. Morph. Ökol. Tiere. 27 518-586.

Pukowski, E. (1934a). Zur Systematik der Necrophorus Larven (Col.) Stettin Ent. Ztg. 95 53-60.

Pukowski, E. (1934b). Die Brutfliege der Totengrabers. Ent. Bl. 30 109-112.

Pukowski, E. (1934c). Oekologisches Beobachtungen an Necrophorus. Ent. Rdsch. 51 3-6.

Putman, R.J. (1977). Dynamics of the blowfly Calliphora erythrocephala within carrion. J. Anim. Ecol. 46 853-866.

Putman, R.J. (1978). The role of carrion frequenting arthropods in the decay process. Ecol. Entomol. (In press).

Rapp, A. (1959). Zur Biologie und Ethologie der Käfermilbe Parasitus coleoptratorum L. 1758. (Ein Beitrag zum Phoresie-Problem). Zool. Jahr. Syst. 86 303-366.

Ratcliffe, B.C. and Leudtke, R.J. (1969). A comparison of silphids taken from covered and uncovered carrion (Coleoptera, Silphidae). Coleop. Bull. 23 103-105.

Reed, H.B. (1958). A study of dog carcass communities in Tennessee with special reference to the insects. Am. Mid. Nat. 59 213-245.

Reid, R.W. (1962). Biology of the mountain pine beetle, Dendroctonus monticolae Hopkins, in the East Kootenay region of British Columbia II : Behaviour in the host, fecundity and internal changes in the female. Can. Ent. 94 605-613.

Reitter, E. (1909). 'Fauna Germanica : Die Käfer des Deutschen Reiches Vol. II '. Lutz, Stuttgart.

Reyes-Castillo, P. and Ritcher, P.O. (1973). Ovariole number in Passalidae (Coleoptera). Proc. ent. soc. Wash. 75 478-479.

Reynoldson, T.B. (1966). The distribution and abundance of lake dwelling triclads - towards a hypothesis. Adv. Ecol. Res. 3 1-71.

Reynoldson, T.B. (1975). Food overlap of lake dwelling triclads in the field. J. Anim. Ecol. 44 245-250.

Reynoldson, T.B. and Bellamy, L.S. (1971). The establishment of interspecific competition in field populations with an example of competition in action between Polycelis nigra (Mull) and P.tenuis (Ijima) (Turbellaria : Tricladida). In. P.G. Den Boer and G.R. Gradwell (Eds.) 'Dynamics of Populations' pp. 282-297. Centre for Agricultural Publishing Documentation, Wagenigen.

Reynoldson, T.B. and Bellamy, L.S. (1973). Interspecific competition in lake dwelling triclads : a laboratory study. Oikos 24 301-313.

Reynoldson, T.B. and Davies, R.W. (1970). Food niche and coexistence in lake dwelling triclads. J. Anim. Ecol. 39 598-617.

Ritcher, P.O. and Baker, C.W. (1974). Ovariole number in Scarabaeoidea (Coleoptera:Lucanidae, Passalidae, Scarabaeidae). Proc, ent. soc. Wash. 76 480-494.

Roehrich, C. (1949). Notes sur les Nécrophores dans le Bocage Normandi. L'Entomol. 5 44-45.

Rogers, L.E., Hinds, W.T. and Buschbom, R.L. (1976). A general weight vs. length relationship for insects. Ann. ent. soc. Amer. 69 387-389.

Rosen, B.R. (1968). The solid geology of Inchcailloch, part of Loch Lomond National Nature Reserve. Unpublished internal report, Nature Conservancy, Edinburgh.

Roubal, J. (1934). Beschreibung zweier neuer Coleopteren nebst Bemerkungen Folia. zool. Hydrobiol. 5 323-5.

Roubal, J. (1939). Fauna Bohemia, Coleoptera Nova. Acta. Soc. ent. Bohem. 36 81-32.

Roubal, J. (1942). De nonnullis nostris Necrophoris Acta. Soc. ent. Bohem. 42 17.

Roussel, J.P. (1963). Conditions de reprise de l'activité et de la reproduction chez Necrophorus vespillo L. en etat d'hibernation. Bull. Soc. Zool. France. 88 671-673.

Roussel, J.P. (1964a). Le development larvaire de Necrophorus vespillo L. Bull. Soc. Zool. France 89 102-110.

Roussel, J.P. (1964b). Le developpment larvaire de Necrophorus fossor Er. Bull. Soc. Zool. France. 89 111-117.

Roussel, J.P. (1965). Rechèrches sur la diapause de Necrophorus fossor Er. Bull. Soc. Zool. France 90 67-87.

Rowlands, J.W. (1969). Reproduction of the Skomer vole. Nature in Wales 11 169-175.

Ryzkowski, L. (1971). Reproduction of bank voles and survival of juveniles in different pine forest ecosystems. Ann. Zool. Fennici. 8 85-91.

Sandhall, Å. (1975). 'Insects and other invertebrates in Colour'. Lutterworth Press, Guildford and London.

Sage, B.L. (1977). The Coleoptera of Skomer Island, Pembrokeshire, and their ecology. Nature in Wales 15 184-208.

Schegoleva-Barovskaya, T. (1933). Les Necrophorini (Coleoptera, Silphidae) de la faune de l'URSS. Trav. Inst. Zool. Acad. Sci. URSS. 1 161-191.

Schneider, P. (1975). Die Flugtypen der Käfer (Coleoptera). Entomol. Germ. 1 222-231.

Schumacher, R. (1973). Beitrag zur Kenntnis der Stridulationsapparate einheimischer Necrophorus arten (Necrophorus humator Ol, N.investigator Zett, N.vespilloides Herbst.) (Insecta : Coleoptera). Z. Morph. Tiere 75 65-75.

Semenov-Tian-Shanshii, A.P. (1933). De tribu Necrophorini (Coleoptera, Silphidae) classificanda et de ejus distributione geographica. Trav. Inst. Zool. Acad. Sci. URSS 1 149-160.

Shibata, T. (1969). Some reports on the burying beetles from Japan I. (Col. Silphidae). Ent. Rev. Japan. 21 47-54.

Shubeck, P.P. (1967). Ecological studies of Necrophagous beetles in Hutcheson Memorial forest (USA). Diss. Abst. 28 (B) 2667.

Shubeck, P.P. (1968). Orientation of beetles to carrion : random or non-random? J. New York ent. Soc. 76 253-265.

Shubeck, P.P. (1969). Ecological studies on carrion beetles in Hutcheson Memorial Forest. J. New York ent. Soc. 77 133-151.

Shubeck, P.P. (1970). Silphidae (Col.): attraction to carrion baited air cans versus carrion baited groundcans. Coleop. Bull. 24 66-70.

Shubeck, P.P. (1971). Diel periodicities of certain carrion beetles (Col. Silphidae). Coleop. Bull. 25 41-46.

Sidor, C. (1967). Prilog proučavanju biologye Necrophorus vespillo L. u Vojvodini. Zbornik Prirod. Nauk. 31 62-71.

Sidor, C. (1970). Rezultati ispitvanja uloge insekta grobara (Necrophorus vespillo L.) u prenošenju bæsnila (Col. Silphidae). Acta Biol. Jugosl. Ser. Mikrobiol. 7 131-138.

Smetana, A. (1943). Duae coleopterorum aberratiores de RČS descriptiones. Acta Soc. Ent. Čsl. 45 34-35.

Snyman, A. (1949). The influence of population densities on the development and oviposition of Plodia interpunctella Hübn (Lepidoptera). J. ent, Soc. S.Afr. 12 137-141.

Solomon, M.E. (1969). 'Population Dynamics' Arnold, London.

Southern, H.N. (1954). Tawny owls and their prey. Ibis. 96 334-410.

Southern H.N. (1964). 'The Handbook of British Mammals'. 1st Edition Blackwell, Oxford.

Southern, H.N. (1970). The natural control of a population of Tawny Owls (Strix aluco) . J. Zool. 162 197-285.

Southwood, T.R.E. (1966). 'Ecological Methods'. Methuen, London.

Southwood, T.R.E. (1975). The dynamics of insect populations. In D. Pimental (Ed.) 'Insects, Science and Society' pp. 151-199, Academic Press, New York.

Southwood, T.R.E. (1977). Habitat, the templet for ecological strategies? J. Anim. Ecol. 46 337-365.

Springett, B.P. (1967). The biology of Necrophorus (Col.) and the mortality of terns (Sterna) : an ecological study. Unpublished, Ph.D Thesis, University of Durham.

Springett, B.P. (1968). Aspects of the relationship between burying beetles Necrophorus spp. and the mite Poecilochirus necrophori Vitz. J. Anim. Ecol. 37 417-424.

Starzyk, J.R. (1967). An interesting case of phoresis of the mite Poecilochirus necrophori (Vitz) (Parasitiformes, Parasitidae) on the burying beetle, Nicrophorus fossor Er. (Coleoptera, Silphidae). Przegl. zool. 11 51-53.

Steele, B.F. (1927). Notes on the feeding habits of carrion beetles. J. New York ent. Soc. 35 77-81.

Stephens, J.F. (1929). 'Manual of British Coleoptera' Longmans, London.

Stoffolano, J.G. (1974). Influence of diapause and diet on the development of the gonads and accessory reproductive organs of the black blowfly, Phormia regina (Meigen). Can. J. Zool. 52 981-933.

Strangeways-Dixon, J. (1961). The relationship between nutrition, hormones and reproduction in the blowfly Calliphora erythrocephala (Meig.) I. Selective feeding in relation to the reproductive cycle, the corpus allatum volume and fertilisation. J. exp. Biol. 38 225-235.

Stubbs, M. (1977). Density dependence in the life cycles of animals and its importance in K- and r-strategies. J. Anim. Ecol. 46 677-688.

Šulc, K. (1940). Ueber die Putzvorrichtungen bei den Necrophoren (Coleoptera). Věstn České Zool. Společ. 8 149-165.

Suzzoni, J.P. (1973). Etude histologique et fonctionnement de l'appareil reproducteur femelle de Phosphuga atrata L. (Coleoptera, Silphidae). Ann. Sci. Nat. Zool. 15 271-292.

Székessy, V. (1961). Zwei neue aberrationem der Silphiden Gattung Necrophorus Fab. (Coleoptera). Folia ent. Hung. 14 (NS) 333-335.

Takahashi, F. (1956). On the effects of population density on the power of reproduction of the almond moth Ephertia cautella I. On the relationship between the body size of the moth and its fecundity and longevity. Jap. Jour. Appl. Zool. 21 77-82.

Thalenthorst, W. (1953). Grundzüge der Populationdynamik der grossen Fichtenborkenkäfers, Ips typographus L. Schr. Reihe. forstl. Fak. Univ. Gothingen. 21 1-126.

Theaker, J. (1976). Some notes on fallow deer (Dama dama) on Inchcailloch. Unpublished Internal Report, Nature Conservancy Council, Balloch.

Theaker, J. (1977). Some notes on the deer population of Inchcailloch, part of Loch Lomond National Nature Reserve. Report published by Nature Conservancy Council, S.W. Scotland Region.

Théorides, J. (1950a). Notes diverses sur les Necrophorus (Coleoptera, Silphidae). Bull. Inst. Sci. Nat. Belge. 26 1-20.

Théorides, J. (1950b). Observations et remarques sur l'ecologie des Nécrophores (Coleoptera, Silphidae). Physiol. comp. oecol. 2 107-125.

Théorides, J. (1955). Contribution a l'étude des parasites et phorétiques de Coléoptères terrestres. Suppl. No.4 'Vie et Milieu'. Bulletin des Laboratoire Arago. pp. 1-310, Herman et Cie, Paris.

Théorides, J. and Van Heerdt, P.F. (1952). Nouvelles recherches écologiques sur les Nécrophores (Coleoptera, Silphidae) : Comparison des resultats du terrain avec ceux du laboratoire (thermopreferendum et hygropreferendum). Oecol. 2 297-309.

Toulon, D. (1971). Les Nécrophores français. Bull. soc. ent. N. France 177 1-3.

Tweedie, M. (1966). Burying beetles. Animals 8 499.

Ullyett, G.C. and Van der Merwe, J.S. (1947). Some factors influencing population growth of Ephestia kühniella Zell (Lep., Phycitidae). J. ent. soc. S.Afr. 10 46-73.

Vagtholm-Jensen, O. (1971). Om indsamling af biller i urtepotter og fangstdåser (Coleoptera). Entomol. Midd. 39 48-50.

Varley, G.C. and Gradwell, J.R. (1960). Key factors in population studies. J. Anim. Ecol. 29 399-401.

Varley, G.C. and Gradwell, G.R. (1968). Population models for the winter moth. In T.R.E. Southwood (Ed.) 'Insect Abundance'. Symp. Roy. Ecol. Soc. Lond. 4 132-142.

Volk, J. (1950). Die nematoden der Regenwürmer und Aasbesuchenden Käfer. Zool. Jahrb. 79 1-70.

Volterra, V. (1926). Variazioni a fluttuazioni del numero d'individui in specie animali conviventi. Mem. Acad. Lincei. 2 31-113.

Von Haartman, L. (1971). Population Dynamics. In D.S. Farmer and J.R. King (Eds.) 'Avian Biology' 1 391-459, Academic Press, London.

Waldow, U. (1973). Elektrophysiologie einer neuen Aasgeruchrezeptors und seine Bedeutung für das Verhalten des Totengräbers (Necrophorus) J. Comp. Physiol. 83 415-424.

Walker, T.J. (1957). Ecological studies of the arthropods associated with certain decaying materials in four habitats. Ecology 38 262-276.

Walsh, G.B. (1931). Studies on the British Necrophagous Coleoptera - 1 Ent. mon. Mag. 67 76-81.

Walsh, G.B. (1933). Studies on the British Necrophagous Coleoptera - 2. Ent. mon. Mag. 69 28-32.

Wasowska, S. (1953). La Morphologie des cornes chez les Coléoptères de la famille Silphidae. S prav. Touv. Nauk. Torum 5 128-30.

Wasti, S.S. (1972). A study of the carrion of the common fowl Gallus domesticus in relation to arthropod succession. J. Georgia Entomol. Soc. 7 221-228.

Wasti, S.S., Hasmer, D.W. and Barney, W.E. (1975). Population density and larval competition in Diptera: I. Biological effects of Intraspecific competition on the three species of muscid flies. Z. Agnew Entomol. 79 96-103.

Waterhouse, D.F. (1947). The relative importance of live sheep and of carrion as breeding grounds for the Australian sheep blowfly Lucilia cuprina. Counc. Sci. Ind. Res. Austr. Bull. 217.

Welch, R.C. (1968). Some coleoptera from Loch Lomond National Nature Reserve. Ent. mon. Mag. 104 119-122.

Welch, R.C. (1973). 'Coleoptera' In R.C. Steele and R.C. Welch (Eds.) 'Monks Wood: a nature reserve record' The Nature Conservancy, The Natural Environment Research Council, Huntingdon.

Wigglesworth, (1965). 'The principles of insect physiology' 8th Edition, Methuen, London.

Wightman, J.A. (1978). The ecology of Callosobruchus analis (Coleoptera, Bruchidae) : morphometrics and energetics of the immature stages. J. Anim. Ecol. 47 117-129.

Williamson, K. (1969). Bird communities in woodland habitats in Wester Ross, Scotland. Quar. Journ. For. 63 305-328.

Williamson, K. (1972). Oak wood breeding bird communities in the Loch Lomond National Nature Reserve. Quar. Journ. For. 68 9-28.

Wilson, E.O. (1971). 'The Insect societies'. Harvard University Press, Cambridge, Mass.

Wilson, E.O. (1975). 'Sociobiology, the new Synthesis'. Harvard University Press, Cambridge, Mass.

Witherby, H.F., Jourdain, F.C.R., Ticehurst, N.F. and Tucker, B. (1933). 'The handbook of British Birds' Witherby, London.

APPENDIX 1

Species of Necrophorus found in Britain. Comparison of Species Lists.

Bishop Collection (University of Glasgow)	Stephens (1839)	Murray (1853)	Hoffmann (1902)
N.germanicus L.	N.germanicus	-	N.germanicus L.
N.humator Goez.	N.humator	N.humator Fab	N.humator Fab
N.mortuorum F. (= vespilloides)	N.mortuorum	N.mortuorum Fab	N.mortuorum F.
N.vestigator Hers	N.sepultor (= vestigator)	N.vestigator Hers.	N.vestigator Hers.
N.ruspator Er. (= investigator)	N.vestigator (= investigator)	-	N.ruspator Er.
N.interruptus Steph.	N.interruptus	-	-
N.vespillo L.	N.vespillo	N.vespillo Fab	N.vespillo L.
-	N.obrutor (= sepultor)	-	-

Joy (1932)	Kloet and Hinks (1945)	Dibb (1943)
-	N.germanicus L.	-
N.humator F.	N.humator Goezo	N.humator
N.vespilloides Hbst.	N.vespilloides Hbst.	N.vespilloides
N.vestigator Hers.	N.vestigator Hers.	N.vestigator
N.investigator Zett	N.investigator Zett.	N.investigator
N.interruptus Steph.	N.interruptus Steph.	-
N.vespillo	N.vespillo L.	N.vespillo

APPENDIX 2

Estimate of population numbers of Necrophorus on Inchcailloch, using method of Jolly (1965).

The steps in calculating a population estimate using Jolly's method are as follows:

1) Tabulate data as in Table 1. n_{ij} = number in ith sample last recaptured in jth sample.
Calculate R_i by summing columns from top to bottom. R_i = number of s_i individuals released from ith sample and subsequently recaptured.

2) Calculate a_{ij} by summing figures in Table 1 (n_{ij}) from left to right. Construct Table 2. a_{ij} = number in ith sample last recaptured in jth sample or before. The underlined figure in Table 2 is the number of recaptures in the ith sample (i.e. on the week on its right) = m_i.
Calculate Z_i by summing i - 1 th column from top to bottom, omitting top entry (= m_i). Z_i = number marked before time i which are not caught in the ith sample, but are caught subsequently.

The remaining data are entered in Table 3 as they are calculated.

3) Calculate $\hat{M}_i$ = estimate of total number of marked individuals in the population at the time of capture of the ith sample (= time i).

$$\hat{M}_i = \frac{s_i \; Z_i}{R_i} + m_i \quad (i = 2, 3 \ldots\ldots \ell - 1).$$

(where ℓ = number of samples, $1 < i < \ell$)

Note: the small number of recaptures limited the number of weeks when estimates could be made in this study, particularly in 1974.

4) Calculate $\hat{\alpha}_i$ = proportion of number of marked animals in the ith sample to number captured in ith sample.

$$\hat{\alpha}_i = \frac{M_i}{n_i} \qquad (i = 2, 3, \ldots\ldots \ell)$$

5) Calculate $\hat{N}_i$ = estimate of total number in the population when ith sample captured.

$$\hat{N}_i = \frac{\hat{M}_i}{\hat{\alpha}_i} \qquad (i = 2, 3, \ldots. \ell - 1)$$

6) Calculate $\hat{\phi}_i$ = probability that an animal alive at the moment of release of the ith sample will survive until the time of capture of the i + 1 th sample, (immigration and death being synonymous).

$$\hat{\phi}_i = \frac{M_i + 1}{\hat{M}_i - m_i + s_i} \qquad (i = i, 2, \ldots\ldots \ell - 2)$$

7) Calculate $\hat{B}_i$ = number of new animals joining the population in interval between the ith and i + 1 th sample, and alive at i + 1.

$B_o = N_1$

$$\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i (\hat{N}_i - n_i + s_i) \quad (i = 2, 3 \ldots\ldots \ell - 2)$$

8) Calculate $\sqrt{[V(\hat{N}_i / N_i)]}$ = standard error of $\hat{N}_i$ due to errors in estimation of $\hat{N}_i$, omitting error component which is due to real variation in population, which recaptures are too few to estimate.

$$\sqrt{[V(\hat{N}_i / N)]} \cdot \sqrt{N_i (N_1 - n_i) \left\{ \left[\frac{(M_i - m_i + s_i)}{M_i} \times \left(\frac{1}{R_i} - \frac{1}{s_i} \right) \right] + \left[\frac{(1 - \alpha_i)}{m_i} \right] \right.}$$

Note : Due to the small number of recaptures, and the resultant obvious errors in the figures, it was not considered worthwhile to calculate quantitatively the variations in estimate of total number, survival rate and immigration rate. For this reason, variances for these parameters were not calculated.

Appendix 2 Table 3(a) (1973)

i	$\hat{\alpha}_i$	$\hat{M}_i$	$\hat{N}_i$	$\hat{\phi}_i$	$\hat{B}_i$	$\sqrt{[V(\hat{N}_i/N_i)]}$
1	-	-	-	-	-	-
2	0	0	-	20.4	-	-
3	0	408	-	0.138	2440	-
4	0.025	61	2440	0.467	-	2648.62
5	0	39.67	-	1.855	5979.50	-
6	0.021	125.57	5979.5	0.683	-1987.00	3786.59
7	0.063	128.8	2044.4	1.222	5516.41	1100.93
8	0.027	216	8000	0.920	-6017.2	4948.42
9	0.200	261.2	1306	-	-	703.93
10	0		-	-	-	-
11	0.223	1063	4766.82	-	-	4710.40
12	0.250		-	-	-	-
13	0.235		-	-	-	-
14	0.208		-	-	-	-
15	0.154		-	-	-	-
16	0.090	72.67	807.44	0.446	3361.75	625.64
17	0.014	52	3714.29	0.382	-13483.52	4598.89
18	0.038	26	684.21	1.75	-	638.61
19	0	56	-	-	-	-
20	0.017		-	-	-	-
21	0.030	311	10366.67	-	-	6126.72
22	0.036		-	-	-	-
23	0.075		-	-	-	-
24				-		
25	0.048	27	562.5	-	-	709.00
26	0		-	-	-	-
27	0.091		-	-	-	-
28	0.333		-	-	-	-
29	0	0	-	-	-	-
30	0		-	-	-	-
31	0.333	-	-	-	-	-

Appendix 2 Table 3(b) (1974)

i	$\hat{\alpha}_i$	$\hat{M}_i$	$\hat{N}_i$	$\hat{\phi}_i$	$\hat{B}_i$	$\sqrt{[V(\hat{N}_i/N_i)]}$
1	-	-	-	-	-	-
2	0		-	-	-	
3	0		-	-	-	
4	0	0	-	-	-	
5	0		-	-	-	
6	0	15.5	-	-	-	
7	0		-	-	-	
8	0.018		-	-	-	
9	0		-	-	-	
10	0	21	-	-	-	
11	0		-	-	-	
12	0.007		-	-	-	
13	0		-	-	-	
14	0	27	-	-	-	
15	0.077		-	-	-	
16	0		-	-	-	
17	0		-	-	-	
18	0.025	61	2440	-	-	2203.07
19	0	72	-	-	-	-
20	0		-	-	-	-
21	0.013	11:5	884.61	0.414	14496.49	1045.01
22	0.006	89	14833.33	-	-	21748.62
23	0		-	-	-	-
24	0		-	-	-	-
25	0.063	92	1460.32	-	-	1899.24
26	0.031		-	-	-	-
27	0.017		-	-	-	-
28	0.038		-	-	-	-
29	0		-	-	-	-
30	0		-	-	-	-
31	0		-	-	-	-
32	0		-	-	-	-
33	0		-	-	-	-

Appendix 2 Table 3(c) (1975)

i	$\hat{\alpha}_i$	$\hat{M}_i$	$\hat{N}_i$	$\hat{\phi}_i$	$\hat{B}_i$	$\sqrt{[V(\hat{N}_i/N_i)]}$
1	-	-	-	-	-	-
2	0	5.31	-	0.691	-	-
3	0	51.33	-	10.268	1377.46	-
4	0.031	640	20645.16	0.170	-	19312.62
5	0.058	123.6	2131.03	-	-	1443.73
6	0.143		-	-	-	-
7	0.048	61.75	1286.46	-	-	1081.30
8	0		-	-	-	-
9	0.077		-	-	-	-
10	0		-	-	-	-
11	0.286	8	27.97	6.00	3032.65	17.87
12	0.017	54	3176.47	1.325	3606.00	3640.17
13	0.018	140.5	7805.55	0.229	-1085.54	9682.33
14	0.056	39	696.43	-	-	584.42
15	0.148		-	-	-	-
16	0.009		-	-	-	-
17	0.006	38	6333.33	0.551	6214.28	9930.94
18	0.004	37.5	9375.00	-	-	14387.4
19	0.010		-	-	-	-
20	0.048	-	-	-	-	-

Appendix 3

Estimate of the carrion available to burying beetles on Inchcailloch

Not enough is known about the ecology of the vertebrates of Inchcailloch to estimate with any accuracy how many corpses will be available to burying beetles on the island. Indeed, such information is available for few areas in the British Isles. By extrapolation from other studies it is possible to estimate when carrion will be available, and what type of corpse will be found. An analysis of this type can provide only a crude estimation of carrion availability for burying beetles however and much work is required to confirm the hypotheses resulting from it. Further studies are also required before any statement at all can be made about the actual numbers of corpses available to burying beetles on Inchcailloch.

1. Deer

Two species of deer are present on Inchcailloch, the fallow (Dama dama L.) and roe (Capreolus capreolus L.). The biology of the two species is different, roe being territorial, while fallow are non-territorial. As a result, their carrion potential is different.

(a) Fallow deer:

Adult fallow range in size from 63.6kg to 110kg (Southern, 1964). The perinatal weight is 4 - 5kg (Chaplin, 1977). The growth of male calves to 19 - 32kg occurs during the first year, and by the third year, young males have reached 50 - 80kg. The population of fallow deer on Inchcailloch during the study period as estimated by Theaker (1976, 1977) is shown in Table 1. An "acceptable" density of fallow deer is 1/70 acres (Southern, 1964). The density on Inchcailloch as estimated by Theaker was 1/12 acres (summer) and 1/3 acres (winter). The population density on Inchcailloch is, therefore, high compared with other areas.

Generally, a single fawn is born in May/June (Southern, 1964), but breeding appears to be later in Scotland, kids being dropped in June/July (R.A. Chaplin, pers. comm.). On Inchcailloch, kids are dropped from mid June until the end of July (Theaker, 1976, 1977). From the figures in Table 1, five young were born in 1973, 4 in 1974 and 4 in 1975.

Mortality of the fallow deer population on Inchcailloch was estimated by Chaplin (pers. comm.). Mortality in fallow is erratic and there may well be years without deaths, particularly in areas where no shooting occurs. If food supply is inadequate an age related mortality will occur, most deaths occurring in early spring when food supply is most limited. Mortality is heaviest among prickets, grown fawns (8 - 9 months old) and among old does and bucks. Deaths in summer are likely to be due to accidental injuries, and these are unlikely to cause more than one or two deaths in ten years. The Inchcailloch population may, therefore, have 1 pricket, 1 doe and possibly 1 fawn each year in early spring.

With an increasing fallow deer population, food may become limiting in winter and mortality increase (R.A. Chaplin, pers. comm.). Theaker (1976, 1977) concludes that Inchcailloch has reached saturation point for fallow deer and the population is not expected to vary a great deal in the future. Theaker (1976) states that the island is not damaged excessively by deer, and suggests that they use the island as a larder for winter feed. This would indicate that food is not a limiting factor for fallow deer on Inchcailloch. Excess numbers seem to move off the island rather than die. The absence of any major fallow deer mortality is supported by Theaker's results (Table 1) and personal observation during this study; no fallow deer corpses were found on Inchcailloch in the three years of the study.

(b) Roe deer:

Male roe deer weigh on average 16kg, and female 11-21kg (Southern, 1964). Chaplin (1977) gives a perinatal weight of 1.3 - 2kg. By 3 - 9 months, fawns are 15 - 20kg and by their second winter weigh 22-26kg.

The roe deer population estimate made by Theaker (1977) is shown in Table 1. The roe deer population is about double that of fallow at c. 30 animals. Southern (1964) states that the peak density of roe is 60 to 65/100ha, and the 'economic' density is 1 per 15/40 acres. The estimated roe population on Inchcailloch is at a density of c 47/100ha (= 1/5 acres). Although not at peak density, this is a high density for roe deer.

Young roe are generally born in late spring (late May - Southern, 1964; May/June - Chaplin, 1977). Birth appears to be slightly later in Scotland, early summer (June 3rd to June 15th) being 'normal' (A. Loudon, pers. comm.). This is the period when most young were born on Inchcailloch (Theaker, 1977). Two young are frequent (Southern, 1964). 11 young were born on Inchcailloch on 1974 and 14 in 1975 (Table 1).

Mortality for the Inchcailloch roe deer was estimated by A. Loudon (pers. comm.). Roe are more territorial than fallow and mortality is more likely to be predictable. Mortality of new born young occurs in the first two weeks of life. This mortality is affected by population density, predation and weather. In the present circumstances, up to six kids might die on the island by the end of June. Buck mortality occurs in late spring and early summer. In this population one buck per year may be replaced as a territorial buck and possibly killed in a fight to the death over territory. Two or three does may die each year on

Table 1

Deer population on Inchcailloch (From Theaker, 1976, 1977).

(a) Fallow

	Winter 1973/74	Summer 1974	Winter 1974/75	Summer 1975	Early Winter 1975
Bucks	2	1	2	1	3
Prickets (yearling bucks)	1	1	3	1	2
Does	7	5	7	5	7
Young/Fawns	5(Y)	4(F)	4(Y)	4(F)	4(Y)
Total population	15	11	16	11	16

(b) Roe

	Winter 1973/74	Summer 1974	Winter 1974/75	Summer 1975	Early Winter 1975
Bucks	3	8	7	8	8
Does	9	8	8	8	8
Juv. Males	5		4		6
Juv.Females	5		7		7
Young		11		14	
Total population	27	27	26	30	29

Appendix 2 Table 1(a) Calculation of N_{ij} (1973)

Week of Capture (i)	Total No. Recapture (n_i)	Total No. Released (s_i)	Week when beetles last Captured (j)
1	1		1
2	29	20	- 2
3	36	34	- - 3
4	40	25	- 1 - 4
5	46	28	- - - - 5
6	143	66	- 2 1 - - 6
7	64	52	- 2 - 2 - - 7
8	111	71	- 1 - - 2 - - 8
9	20	22	- 1 - - 1 2 2 - 9
10	4	0	- - - - - - - - - -10
11	103	26	- 2 - - 5 4 4 7 1 -11
12	32	14	- 1 - 1 1 2 1 2 - - -12
13	17	5	- - - - - 3 - 1 - - - -13
14	24	1	- - - - - - 2 2 1 - - - -14
15	91	47	- 2 - 1 2 1 3 2 2 - 1 - - -15
16	67	50	- - - 1 1 2 2 - - - - - - - -16
17	71	17	- - - - - - 1 - - - - - - - -17
18	53	8	- - - - - - - - 1 - - - - - - 1 -18
19	242	84	- - - - - - - - - - - - - - - - - - -19
20	60	27	- - - - - - - - 1 - - - - - - - - - -20
21	345	225	- - - - - - - - 1 - - - - - - - 2 1 1 6 -21
22	110	12	- - - - - - - - - - - - - - - - - 1 1 2 - -22
23	67	15	- - - - - - - - - - - - - - - - - - - 3 - 2 -23
24			-24
25	84	23	- - - - - - - - - - - - - - - - - - - 1 - 3 - - -25
26	38	6	- -26
27	11	6	- 1 -27
28	3	0	- 1 - - - - - -28
29	27	22	- -29
30	10	8	- -30
31	3	0	- 1 -31

R_i = 0 12 1 5 12 14 15 16 5 0 1 0 0 0 0 3 2 2 12 0 6 0 0 0 1 0 0 0 1 0

Appendix 2 Table 1(b) Calculation of N_{ij} (1974)

Week of Capture (i)	Total no. captured (n_i)	Total no. released (s_i)	Week when beetles last captured (j)
1	2	2	1
2	14	10	- 2
3	16	12	- - 3
4	45	24	- - - 4
5	37	30	- - - - 5
6	36	31	- - - - - 6
7	35	71	- - - - - - 7
8	55	42	- - - - - - 1 8
9	62	22	- - - - - - - - 9
10	15	7	- - - - - - - - -10
11	14	4	- - - - - - - - - -11
12	146	2	- - - - - 1 - - - - -12
13	6	1	- - - - - - - - - - - -13
14	20	18	- - - - - - - - - - - - -14
15	13	8	- - - - - - - - - 1 - - - -15
16	3	0	- - - - - - - - - - - - - - -16
17	2	1	- - - - - - - - - - - - - - - -17
18	118	116	- - - - - 1 - - - - - - - 2 - - -18
19	44	24	- - - - - - - - - - - - - - - - - -19
20	106	21	- - - - - - - - - - - - - - - - - -20
21	78	7	- - - 1 - - - - - - - - - - - - - -21
22	164	22	- - - - - - - - - - - - - - - - 1 - - -22
23	12	3	- - - - - - - - - - - - - - - - - - - -23
24	28	7	- - - - - - - - - - - - - - - - - - - -24
25	32	30	- - - - - - - - - - - - - - - - 1 - - 1 - - -25
26	32	26	- - - - - - - - - - - - - - - - - 1 - - - -26
27	60	43	- - - - - - - - - - - - - - - - 1 - - - - - -27
28	52	52	- - - - - - - - - - - - - - - - - - 1 - - 1 - -28
29	14	13	- -29
30	18	12	- -30
31	12	8	- -31
32	3	3	- -32
33	1	0	- -33

R_i = 0 0 0 1 0 2 0 0 0 1 0 0 0 2 0 0 0 2 1 0 2 1 0 0 1 0 0 0 0 0 0 0

Appendix 2 Table 1(c)

Calculation of N_{ij} (1975)

Week of capture (i)	Total No. captures (n_i)	Total No. released (s_i)	Week when beetles last captured (j)
1	6	6	1
2	109	61	- 2
3	13	11	- - 3
4	98	91	- 3 - 4
5	69	46	- 1 3 - 5
6	70	67	1 7 - - 2 6
7	83	77	- 1 - 2 1 - 7
8	25	14	- - - - - - - - 8
9	13	4	- - - - 1 - - - 9
10	4	2	- - - - - - - - - -10
11	7	3	- 1 - - 1 - - - - -11
12	68	53	- - - - - - - 1 - - - -12
13	55	31	- - - - - - - - - - 1 -13
14	54	9	- - - - - - 1 - - - - 2 -14
15	27	2	- - - - - - - 1 - - - 1 1 1 -15
16	106	21	- - - - - - - - - - - - - 1 - -16
17	631	34	- - - - - - - 1 - - - - 1 - 2 - -17
18	236	73	- - - - - - - - - - - - 1 - - - - -18
19	95	32	- - - - - - - - - - - - - - - - - - 1 -19
20	42	17	- 2 -20
	R_i =		1 1 3 3 2 5 0 4 0 0 0 2 5 2 2 0 0 1 2 0

Appendix 2 Table 2(a)

Values of a_{ij} (1973)

1	1																														
2	0	2																													
3	0	0	3																												
4	0	1	1	4																											
5	0	0	0	0	5																										
6	0	2	3	3	3	6																									
7	0	2	2	4	4	4	7																								
8	0	1	1	1	3	3	3	8																							
9	0	1	1	1	2	4	6	1	9																						
10	0	0	0	0	0	0	0	0	0	0	10																				
11	0	2	2	2	7	11	15	22	23	23	11																				
12	0	1	1	2	3	5	6	8	8	8	8	12																			
13	0	0	0	0	0	3	3	4	4	4	4	4	13																		
14	0	0	0	0	0	0	2	4	5	5	5	5	5	14																	
15	0	2	2	3	5	6	9	11	13	13	14	14	14	14	15																
16	0	0	0	1	2	4	6	6	6	6	6	6	6	6	6	16															
17	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	17														
18	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	2	2	18													
19	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	19												
20	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	20												
21	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	3	4	5	11	11	21										
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	4	4	4	22									
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	4	5	23								
24	———																						24								
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	4	4	4	25						
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26					
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	27				
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	28				
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29				
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30			
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	31
Z_i =	0	12	12	17	26	36	48	58	63	40	33	24	24	10	4	6	6	8	19	8	10	5	5	1	2	1	0	0	1	0	

Appendix 2 Table 2(b) Values of a_{ij} (1974)

1	1	
2	0	2
3	0 0	3
4	0 0 0	4
5	0 0 0 0	5
6	0 0 0 0 0	6
7	0 0 0 0 0 0	7
8	0 0 0 0 0 0 1	8
9	0 0 0 0 0 0 0 0	9
10	0 0 0 0 0 0 0 0 0	10
11	0 0 0 0 0 0 0 0 0 0	11
12	0 0 0 0 0 1 1 1 1 1 1	12
13	0 0 0 0 0 0 0 0 0 0 0 0	13
14	0 0 0 0 0 0 0 0 0 0 0 0 0	14
15	0 0 0 0 0 0 0 0 0 1 1 1 1 1	15
16	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	16
17	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	17
18	0 0 0 0 0 1 1 1 1 1 1 1 1 3 3 3	18
19	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	19
20	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	20
21	0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	21
22	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1	22
23	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	23
24	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	24
25	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 2 2 2	25
26	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1	26
27	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1	27
28	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 2 2	28
29	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	29
30	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	30
31	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	31
32	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	32
33	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	33

Z_i = 0 0 0 1 1 3 3 3 3 4 3 3 3 4 4 4 1 3 4 3 4 5 5 3 3 2 0 0 0 0 0 0

Appendix 2 Table 2(c) Values of a_{ij} (1975)

1	1																		
2	0	2																	
3	0	0	3																
4	0	3	3	4															
5	0	1	4	4	5														
6	1	8	8	8	10	6													
7	0	1	1	3	4	4	7												
8	0	0	0	0	0	0	0	8											
9	0	0	0	0	1	1	1	1	9										
10	0	0	0	0	0	0	0	0	0	10									
11	0	1	1	1	2	2	2	2	2	2	11								
12	0	0	0	0	0	0	1	1	1	1	1	12							
13	0	0	0	0	0	0	0	0	0	0	1	1	13						
14	0	0	0	0	0	0	1	1	1	1	1	3	3	14					
15	0	0	0	0	0	0	1	1	1	1	2	3	4	4	15				
16	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	16			
17	0	0	0	0	0	0	1	1	1	1	1	2	2	4	4	4	17		
18	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	18	
19	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	19
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	20
z_i =	1	14	14	13	7	3	7	6	6	4	5	9	8	6	5	1	1	2	2	0

Inchcailloch. In Cheddington, Dorset, doe mortality occurred in late winter, February/March. Some yearling and non established deer will be forced to emigrate from the island by territorial aggression from late spring to mid summer. Some of these animals may die, although when they die is not known.

That roe mortality on Inchcailloch is higher than that of fallow is confirmed by personal observation. During the course of the study two roe corpses were seen on the island, one buck (June, 1975) and one doe (May, 1974). Several animals have also been killed by poachers over the last few years (C. Placido, pers. comm.) and from April to June 1976, three roe were found dead. Two of these were pregnant females who had accidentally disembowelled themselves while jumping over low branches (C.Placido, pers. comm.).

As with fallow, the roe population on Inchcailloch is believed to be stable (Theaker, 1977). The number of deer corpses potentially available to Necrophorus is therefore unlikely to vary greatly from year to year. The size of deer corpse potentially available will range from 1.8kg (roe fawn) to 110kg (fallow buck). As far as the breeding of Necrophorus is concerned, only the corpses found from late April to late September are significant. During this period, the main regular input of corpses is likely to come from roe deer, with possibly up to 6 kids and 1 buck dying. In addition there will be an irregular and unpredictable supply of one or two adult fallow and roe dying each year due to accidents or shooting. Rarely there may be a fallow fawn dying at birth. These will be the only deer corpses available for breeding Necrophorus.

2. Small mammals

The following small mammals have been recorded from Inchcailloch (East, 1964; Placido, 1971; Mitchell, 1974). Bank voles (Clethrionomys glareolus Schr), field vole (Microtus agrestis L.), common shrew (Sorex araneus L.), mole (Talpa europaea L.) grey squirrel (Sciurus carolinensis Gm), stoat (Mustela erminea L.), Daubenton's bat (Leuconoë daubentonii Leisler).

No reliable data is available on the absolute or relative numbers of each species. Grey squirrels arrived on Inchcailloch in c. 1970 and are relatively uncommon (C. Placido, pers. comm.) Only two sightings of the stoat were made in three years (Placido, 1971), and only one colony of Daubenton's bat has been discovered on the island (Mitchell, 1974). Therefore, these species are likely to be of little importance as far as Necrophorus is concerned.

The results of small mammal trapping on the island (East, 1964; Placido, 1971) suggest that the bank vole is the most common species present, forming most of the catch (East: 89.5%; Placido: 95%). The common shrew and field vole comprised the rest of the catch in equal proportions. Personal examination of tawny owl (Strix aluco) pellets showed a similar relationship - 95% bank vole and 5% shrew remains being found. No field voles were found in owl pellets. These figures should not be accepted completely however. The breakback and Longworth traps commonly used in the trapping estimates are designed to catch voles, and not shrews (C. Placido, pers. comm.). As a result, shrew numbers are underestimated. Using traps designed for shrews, Placido (unpublished data) obtained a shrew density for one particular area of ten times that estimated previously using Longworth traps. Tawny owl pellets may also underestimate the number of shrews in an area, as the

owls catch very few shrews, possibly because of their unpalatability (C.Placido, pers. comm.). In Wytham Wood, tawny owls took only 5% by weight of shrews in their total diet (Southern, 1954, 1970). As both trapping and pellet studies underestimate the relative number present, shrews are probably more common in the study area than would appear from the data available. It is not possible to say whether they are more abundant than bank voles.

As field voles occupy the marginal habitats not occupied by the bank voles on Inchcailloch, trapping results are believed to reflect the relative density of field voles on the island (C. Placido, 1971). Therefore as far as relative densities of small mammals are concerned, it is only possible to say that shrews and bank voles are the most common species, field voles are less common and the other small mammal species are relatively scarce. Placido (1971) trapped 41 bank voles in 1600 sq. metres, which would suggest a bank vole density of c. 250/ha in some parts of the island. Elsewhere, bank voles are recorded in densities of 12-74/ha in woodland (Corbett and Southern, 1977). On Skomer Island (Pembrokeshire) densities of 210/ha are recorded (Fullager, Jewell and Lockley, 1963). Mellanby (1973) records 64/ha in Monks Wood. Shrews have been trapped in densities of 49/ha in British woods (Crowcroft, 1957) and 12-13/ha in sand dunes in Holland (Corbet and Southern, 1977).

(a) Shrew: (Data from Southern, 1964 unless otherwise specified)

Immature shrews in June/July weigh c. 7gms and at sexual maturity the following May, weigh c. 10gms. Breeding of shrews occurs from May until August/October. The number of litters each season varies and although five litters is probably maximum, two per season may be normal due to female mortality. The number of youngper litter is 7-3.

Peak population numbers occur from June to August, when both adults and their progeny are present in the population. Adults die off after breeding, from late summer to early autumn. Mortality of young shrews is 25% for the first four months of life (May/August to August/November) and is then 14% up to the age of 10 months. At 11 months, (April/July of the following year) there is heavy mortality associated with the onset of breeding. At the age of nine months, the mean expectation of further life is three months. Southern (1964) suggests that food supply affects the population but Pernetta (1976) showed that there is abundant food for shrews in Wytham Wood during the period April/August.

Fluctuations in shrew populations occur from year to year but these are not so violent as among rodent populations. In the absence of further data it is not possible to say how the availability of shrew corpses will vary from year to year.

(b) Bank vole. (data from Southern, 1964 unless otherwise specified).

Adult bank voles in summer may weigh 30gms and in winter 16 - 22gms. The breeding season of the bank vole is from mid April until September although in some years, bank voles may breed until December. The animals trapped by East (1964) on 16/17 November were still breeding. The number of litters each year is 4 - 5, and there are 4 - 5 young in each litter (Ryszkowski, 1971). Young are weaned at 2½ weeks, and may reach sexual maturity by 4 - 5 weeks. There may be two generations during the summer. The first generation becomes quickly mature in spring and produces second generation. They grow slowly during the summer, do not become sexually mature and form the bulk of the overwintering population.

In the population studied by Leslie, Chitty and Chitty (1953) in Wales, the death rate was highest from April to July, with a peak in June. The dilution rate from breeding was enough to keep the net population size relatively stable until July/September when there was an influx of young born during the latter part of the breeding season. The death rate fell considerably during the period July to September. Ryszkowski (1971) in Poland showed that survival of juveniles of the spring generation was lower than survival of juveniles of the summer generation.

Bank vole populations vary in size from year to year (Leslie et al., 1953; Southern, 1964; Ryszkowski, 1971), although not so greatly as do field vole populations. The death rate in May/June also varies from year to year (Leslie et al., 1953). As a result of population fluctuations and variations in mortality, there may be variation in the numbers of corpses available to Necrophorus from year to year.

(c) Other species:

Field voles weigh 15 -52 gms. and their biology resembles that of bank voles in many ways. Breeding occurs from April to September. Leslie et al. (1953) suggest the main dilution of the population occurs from July to October, as in bank voles. The highest death rates occur from April to June, with a peak in May. The death rate in May is possibly due to mortality of overwintering first generation adults or juveniles produced by the first generation. Probably both types of mortality are involved as in the bank voles. There may be variations in mortality from year to year and field vole populations are liable to considerably fluctuations.

Moles weigh 65-120gms. As moles live underground for most of the time, except when juveniles are dispersing in the summer, the corpses of those dying would probably not be available for Necrophorus. Nothing is known of the density of moles on Inchcailloch.

3. Birds.

The breeding birds present on Inchcailloch during May and June 1972 were recorded by Williamson (1974). The birds present in Williamson's census plots of Inchcailloch West (17ha) and Inchcailloch East (10ha) are arranged in order of abundance in Table 2, together with their mean weight (Cousins, 1973), the approximate date when young leave the nest and the number of eggs laid (Witherby, Jourdain, Ticehurst and Tucker, 1938).

The density of breeding birds in the census plots was 16 pairs per ha (Inchcailloch West) and c. 13 pairs per ha (Inchcailloch East). The total number of breeding species was 34. The young of 24 of these species leave the nest in May and June and the rest fledge their young during July and August. 15 species have two or more broods and so will have young which leave the nest later in the summer. The mean weights of the ten most common species range from 8.9 to 92.3 gms.

Few studies are available of the mortality of British birds and when it occurs (R. Fuller, pers. comm.). The studies which have been made are not necessarily applicable to Inchcailloch but may give some idea of the periods when mortality is likely to occur.

(a) Willow Warbler (Crampe, 1955). Breeding success from egg laying to fledging was 59.6% for clutches laid in May and 55.8% for clutches started in June. No estimates are given for survival after fledging.

Table 2. Breeding Birds of Inchcailloch

Species [1]	Number of pairs [1] Inch West (17ha)	Inch East (10ha)	Total pairs on census plots	Mean [2] weight (gms)	Approx. [3] date of fledging	Number [3] of eggs
Chaffinch, Fringilla coelebs	47	24	71	22.0	May/June	4 - 5
Wren, Troglodytes troglodytes	38	22	60	9.9	Mid May+	5 - 6
Willow warbler, Phylloscopus trochilus	34	6	40	8.9	Mid June	6 - 7
Blackbird, Turdus merula	24	9	33	92.3	May-Aug.++	4 - 5
Robin, Erithacus rubicula	20	12	32	19.3	April/May++	5 - 6
Song thrush, Turdus philomelos	17	1	18	79.9	May +	4 - 5
Blue tit, Parus caeruleus	13	7	20	10.7	Mid June	7 -14
Coal tit, Parus ater	7	7	14	10.3	Mid June+	7 -11
Great tit, Parus major	7	7	14	18.7	Mid June	6 -11
Garden warbler, Sylvia borin	13	2	15	18.0	Late June	4 - 5
Tree creeper, Certhia familiaris	5	4	9	9.3	May/June+	6
Long tailed tit, Aegithalos caudatus	4	3	7	8.6	Late May+	8 -12
Wood warbler, Phylloscopus sibilatrix	4	3	7	10.1	Late June+	6 - 7
Tree pipit, Anthus trivialis	4	2	6	21.2	June/July+	4 - 6
Common sandpiper, Actitis hypoleucus	4	2	6	65.9	July/Aug.	4
Redstart, Phoenicurus phoenicurus	3	1	4	14.7	Mid June+	6
Spotted flycatcher, Muscicapa striata	3	1	4	15.5	June/July	4 - 5
Pheasant, Phasianus colchicus	2	1	3	1075	May/June	8 -15
Woodpigeon, Columba palumbus	2	2	4	480	May/Oct++	2
Cuckoo, Cuculus canorus	2	1	3	110	-	-
Greater spotted woodpecker Dendrocopos major	2	1	3	77.9	Mid July	4 - 7
Goldcrest, Regulus regulus	3	-	3	5,5	June/July+	7 -10
Starling, Sturnus vulgaris	3	1	4	77.4	Late May	5 - 7
Mallard, Anas platyrhynchos	1	1	2	1010	April	10 -12
Red breasted mergames, Mergas serrator	1	1	2	1006	Mid July	7 -12
Buzzard, Buteo buteo	1	1	2	982	July/Aug	2
Woodcock, Scolopax rusticola	2	-	2	267	May-June+	4
Tawny Owl, Strix aluco	1	-	1	427	May	2 - 4
Carrion crow, Corvus corone	-	1	1	572	July	4 - 5

continued/

Table 2 (continued)

Jay, Garrulus glandarius	-	2	2	167	June	5 - 6
Mistle thrush, Turdus viscivorus	1	1	2	118	April/May+	4
Black cap, Sylvia atricapilla	2	-	2	17.4	Mid-late June	5
Dunnock, Prunella modularis	2	-	2	21.4	April/Aug+	4 - 5
Bullfinch, Pyrrhula pyrrhula	-	2	2	21.8	July+	4 - 5
Total pairs on census plot	=	272	128	400		

+ Bird may have second brood or more (++) in summer

1. Williamson (1974)
2. Cousins (1976)
3. Witherby, Jourdain, Ticehurst and Tucker (1938).

(b) Great tit (Lack, 1966). Most of the annual fluctuations in the breeding populations of the great tit in Marley Wood are due to variations in juvenile mortality before the winter. Most of the juvenile mortality probably occurs during the first one to three weeks after the young leave the nest. The later juveniles leave the nest, the lower is their weight and the higher their mortality. Mortality is due to starvation during the lean period which occurs after the juveniles have left the nest. The mortality of those leaving the nest at the beginning of July is twice that of those leaving the nest at the beginning of June. Most of the nortality due to undernourishment in the nest occurs before mid July, c. 16% of nestlings died in the nest in Marley wood, and 3% in Wytham. A similar mortality pattern is observed for the blue tit.

(c) Coal tit. (A. Deadman, pers. comm.). There is a high post-fledging juvenile mortality in late June-July, although the highest juvenile mortality occurs in late autumn. All juveniles dying do so before November.

(d) Song thrush (Hartley, 1967). At the beginning of the breeding season (March/April), the whole clutch may hatch in a single day. Mortality of clutches laid early in the season is likely to be low. During the summer, hatching may be spread over two or more days. Chicks 24 hours younger than the rest of the brood may survive well unless weather is very unfavourable. A chick 48 hours younger than the majority is unlikely to survive. Dead nestlings are removed from the nest. Nestlings weigh c. 6gms at hatching, c. 10gms at day 5 and by day 9 weigh c. 50gms. The weightat fledging (day 14) is c. 60gms. Undernourished nestlings may die at any time during development. After fledging, the young are fed by their parents for up to 3 weeks. They wait in the same place for feeding, and any scattering of the brood can lead to mortality, as the parents may not be able to find the young to feed them.

(e) Chaffinch (Newton, 1972). Young chaffinches are fed by their parents when they leave the nest. During this period they are dispersed and hidden. The young may be dependent on their parents for food for up to three weeks. Mortality may occur if the young lose contact with their parents or if the weather is severe.

(f) Blackbird (Batten, 1973). The overall mortality of adult blackbirds in Southern England is c. 35%. The highest adult mortalities occurred from March to June, 20% of adults dying during this period. From July to October, 6% of adults died. Survival of juveniles after leaving the nest is 50% but when this mortality occurs is not recorded. The mean number of fledglings per pair per year is 2.6, and the mean number of juveniles per pair per year is 1.69.

Mortality in birds may occur among adults, nestlings and juveniles on leaving the nest. Little is known about patterns of adult mortality for the species present on Inchcailloch. Mortality of nestlings will occur in most Inchcailloch species before June. For the species with two or more broods in a year, however, nestling mortality will occur throughout the summer. Periods of cold or wet weather will increase nestling mortality, either directly or through the food supply (Fox, 1976). If dead nestlings are removed from the nest they may become available to Necrophorus. The weight of dead nestlings will vary with the state of development when death occurred.

The studies that have been carried out suggest that juvenile mortality may be a major source of mortality in birds. In some cases, it has been shown that this mortality occurs soon after the young leave the nest, when they are most vulnerable to starvation and adverse physical conditions. More than half the species of birds on Inchcailloch fledge their young during May and June. Of the ten most common species, five fledge their young from May onwards and five do not

fledge their young until June. Most juvenile mortality may occur from June onwards therefore. In most recorded cases, juvenile mortality occurs mainly before the winter. As a result, juvenile mortality of birds on Inchcailloch may be occurring from June until possibly November.

Bird mortality varies from year to year, depending on the availability of food. For insectivorous species, variations in numbers of oak-defoliating caterpillars has been shown to be of importance in causing variations in nestling and juvenile mortality (Lack, 1966). Variations in numbers of these caterpillars were observed on Inchcailloch during the study. As the ten most common bird species are all insectivorous, this variation may have led to variations in mortality from year to year.

4. Conclusions: Availability of carrion for the three Necrophorus species.

Necrophorus vespilloides, N.humator and N.investigator need carrion at different times. N.vespilloides and N.humator require corpses from April until July, while N.investigator uses carrion for breeding from July until September. The availability of carrion in the study area during these periods is different. From April to July, the carrion is likely to consist of the corpses of juvenile shrews (7gms), adult shrews (10gms), adult and juvenile bank voles (10 - 30gms), adult and juvenile field voles (10 - 30gms) and nestling birds of varying sizes. From July until August, the carrion available to Necrophorus will consist of juvenile and adult shrews and fledgling birds, most weighing less than 20gms. Numerically, birds seem less important than small mammals, birds having a density of c. 15 pairs/ha (Williamson, 1974) compared

with a possible bank vole density of c. 250/ha in some areas (Placido, 1971). As a result, the contribution of birds to the overall number of corpses may be less important than that of small mammals.

Corpses may be fewer in number and less variable in size from July to August than from April to July. Potentially, therefore, more corpses may be available to N.vespilloides than to breeding N.investigator. With the absence of larger bank voles, the corpses that are available to breeding N.investigator will be smaller than those available to breeding N.vespilloides.

N.humator is believed to breed mainly on large corpses (Portevin, 1926a). The requirements of N.humator for carrion are therefore different from those of the other species. The only large corpses suitable for N.humator on Inchcailloch are those of deer. Most deer corpses that do occur, are likely to occur during the breeding season of N.humator from April to July. About three adult and six fawn corpses are estimated to occur on Inchcailloch each year.

Appendix 4.

Defining the Prepupa

The prepupal phase is the only stage in the development of Necrophorus that can not be defined by a specific event, such as egg hatch or moulting. The prepupal stage is part of the third instar, occurring some time before the third moult. During this period, the larvae increase in size, then stop feeding. After a short time without feeding, larvae disperse from the corpse and pupate. Development of the prepupa will be coordinated with this behaviour.

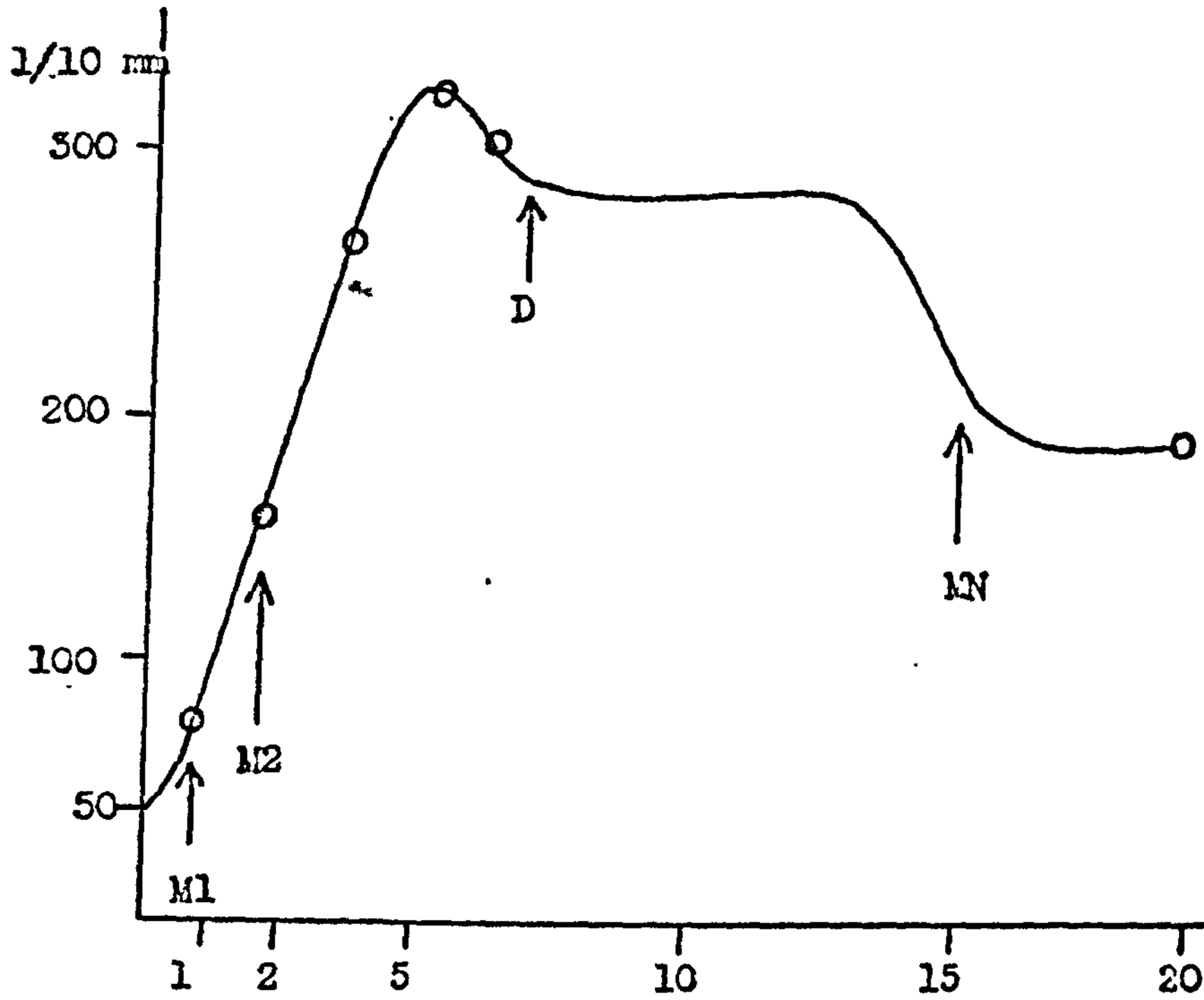
The definition of prepupa to be followed is that of Imms (1959). The prepupa (= pharate pupa) is not a distinct instar, but is the stage during which a larva prepares for the transformation into a pupa. The larval cuticle becomes separated from the hypoderm, and the pupa comes to lie within the persistent larval cuticle. The prepupa therefore differs in external appearance from earlier larvae. During the prepupal period the insect is quiescent, does not feed and becomes contracted and depressed. Pukowski (1933)) defines the prepupal stage in Necrophorus as starting when the larvae leave the corpse. This marks 'a change in condition of the larvae'. Roussel (1964a) uses the same definition. Springett (1967) states, somewhat unhelpfully, that the prepupa is the 'third instar larvae with the gut cleared'. No evidence is offered for these definitions and neither was found to be particularly useful. Examination of growth curves suggests that the definition of Pukowski (1933) and Roussel (1964a) may, in fact, be incorrect. Roussel (1964a) states that at the start of the prepupal stage, the larvae becomes broader, flatter and shorter. As the prepupal stage is defined as starting when the larvae leaves the corpse, this change in length might be expected to occur on dispersal. Examination of Roussel's figs. 3 and 4 (reproduced here in fig. 1) however, shows that most of the decrease

in length occurs before the larva leaves the corpse. Comparison of the two graphs shows that the decrease in length starts at exactly the same time as the decrease in weight begins. The decrease in weight starts when the larva stops feeding. The decrease in length, therefore, must also begin when the larva stops feeding. This would suggest that the prepupal stage, which was defined by Imms (1959) and Roussel (1964a) as starting when the larva starts to become shorter, actually begins when the larva stops feeding. Indeed it may be suggested that the end of feeding is caused by the hormonal changes associated with the start of the prepupal stage. Imms (1959) states that the insect does not feed during the prepupal stage and Springett (1967) confirms that no feeding occurs.

The hypothesis that the onset of the prepupal stage causes termination of feeding of larvae explains an otherwise difficult observation. If the prepupal stage begins when larvae leave the corpse, it is not clear why larvae should remain on the corpse without feeding for 1 - 2 days before leaving the corpse and becoming prepupae. If, however, the onset of the prepupal stage causes the larvae to stop feeding, the period of 2 days 'rest in the corpse' may be seen as necessary for the charges in size etc. associated with the development of the prepupa, to take place. No movement will be possible during this quiescent stage - or 'transformation period'. Once the changes have occurred, movement will become possible, and the larvae (prepupae) will be free to move away from the corpse and from pupal chambers - the 'dispersal period'.

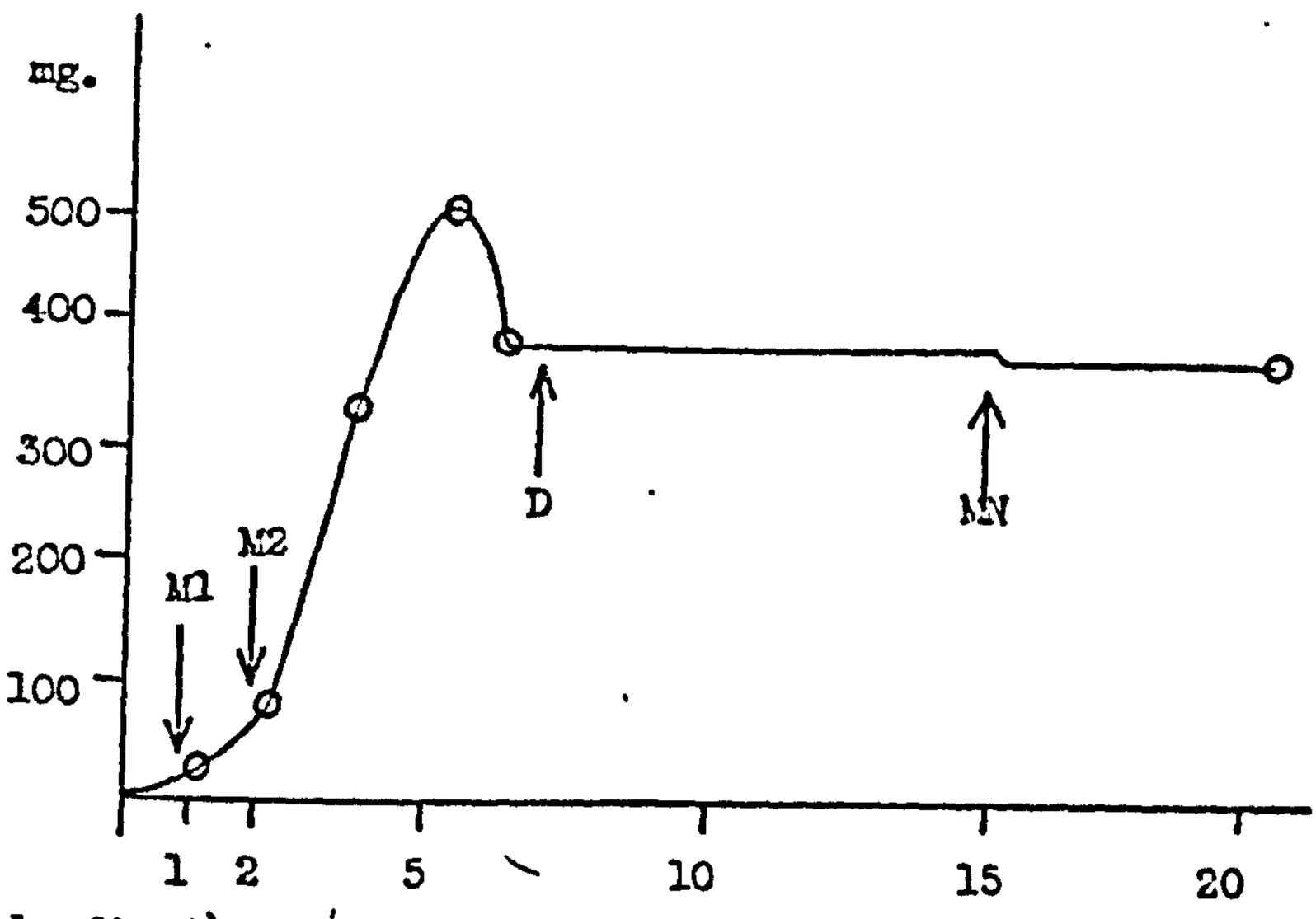
Appendix 4 Figure 1

Growth curves of N.vespillo (from Roussel 1964a.)



(Roussel, fig.3).

Mean curve of increase in length of Necrophorus vespillo from hatching to pupation.



(Roussel, fig.4).

Mean curve of increase in weight of Necrophorus vespillo from hatching to pupation.

M1 = Moult 1; M2 = Moult 2; MN = Pupation.
D = Larvae leave corpse, i.e. start of prepupal stage using definition of Pukowski (1933), Roussel (1964a).

Appendix 5.

Distribution of prepupae on dispersal

The distribution of prepupae after dispersal in the lumped clutch experiment (4.3:1.2.) was analysed using the method of Clark and Evans (1954) as described by Edgar and Meadows (1969). The mean distance to the nearest neighbour in the experiment ($\bar{r}_o$) = 2.56. The mean distance to the nearest neighbour in a randomly distributed population of the same density ($\bar{r}_e$) was calculated.

$$\bar{r}_e = \frac{1}{2(\sqrt{P})}$$

where P = population density = number of larvae ÷ area of container. As the larvae did not spread randomly throughout the container used, the use of the whole container to estimate density would have distorted the result and shown aggregation near the corpse. The maximum distance travelled by a larva was 42cm, therefore the population density was calculated using the area of travel, which was taken to be a circle of radius 42cm.

Area of circle = πr^2 = 5541.77 sq. cm

No. of larvae = 100

Density = P = $\frac{100}{5541.77}$ = 0.018/sq. cm.

$$\bar{r}_e = \frac{1}{2(\sqrt{0.018})} = 3.727$$

The significance of the difference between r_o and r_e was calculated:

$$d = \frac{\bar{r}_o - \bar{r}_e}{\theta / r_e}$$

where $\frac{\theta}{r_e} = \frac{0.26136}{\sqrt{(NP)}}$

where n = number of measurements = 100

$$P = 0.013$$

$$\frac{\theta}{r_e} = \frac{0.26136}{\sqrt{(100 \times 0.013)}} = 0.1948$$

$$d = \frac{2.56 - 3.727}{0.1948}$$

$$= -5.99$$

The probability of observing a departure from the mean value of -5.99 is calculated from Table I of Fisher and Yates (1963) as < 0.001. This value shows that the population is not randomly spaced out but is aggregated.